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Ochre-fronted Antpitta, *Grallaricula ochraceifrons*, a new species from Peru (male, left; female, right). Gouache and acrylic painting by John P. O'Neill.
GRALLARICULA OCHRACEIFRONS, A NEW SPECIES OF ANTPITTA FROM NORTHERN PERU

GARY R. GRAVES, JOHN P. O’NEILL, AND THEODORE A. PARKER, III

In a review of new avian species described in the years 1956–1965, Mayr (1971:315) stated “South America, in particular, seems inexhaustible and has produced almost as many novelties (16) as the rest of the world (19). Indeed, it seems probable that, in the future, it will produce more novelties than all other continents and island regions together.” This prediction was correct during the past decade. If the number of new species discovered per unit time is a crude measure of the “unknown quality” of an avifauna, the Andean region may be the major, and perhaps the last frontier in avian alpha taxonomy.

In August 1976, we collected a strikingly patterned Grallaricula antpitta near Abra Patricia, Dpto. San Martín, Peru. We propose to name this new species

Grallaricula ochraceifrons sp. nov.

OCHRE-FRONTED ANTPITTA

HOLOTYPE.—Louisiana State University Museum of Zoology No. 81998; adult male from 10 km (by road) below (NE) Abra Patricia, elev. approx. 1890 m (6200 ft) 5°46’S, 77°41’W; Dpto. San Martín, Peru, 30 August 1976; prepared by John P. O’Neill, original number 5715.

DIAGNOSIS.—A large, sexually dimorphic Grallaricula antpitta with heavily streaked breast and distinct black malar streaks (see frontispiece). Males differ from males of G. flavirostris, G. nana, G. peruviana, G. lineifrons, and G. loricata in having an ochaceous buff forecrown and dark hindcrown, rather than an olivaceous brown, ochaceous, or gray crown. The only known female is similar to females of G. peruviana but lacks buffy precocular spots (Fig. 1). G. ochraceifrons and G. peruviana appear to be the only sexually dimorphic species in the genus.

DESCRIPTION OF HOLOTYPE.—Wide eye ring ochaceous buff with indistinct dusky crescent extending from gonys upward around anterior portion of eye ring; forecrown and indistinct superciliary ochaceous buff; hindcrown, mantle, rump, and tail dark olivaceous brown; auriculars olivaceous brown with buffy bases; outer web of outermost primary and alula light ochaceous buff; primary edges light olivaceous brown; primary coverts blackish-
brown; axillars and carpal coverts light ochraceous buff. A thin buffy-white malar mark, bordered above and below by black, extends from the base of the bill posteriorly to lower lateral throat region; center of throat white, tinged faintly with buff and bordered laterally with black and buff feathers; feathers of upper breast and sides buff bordered laterally with wide black margins, producing a heavily streaked appearance; lower flanks indistinctly streaked olivaceous brown and dark brown; center of lower breast, belly, and undertail coverts white. Soft parts in life: iris dark brown; maxilla black, distal half of mandible black, light pink basally; tarsi and feet grayish pink.

DISTRIBUTION.—Presently known only from subtropical cloud forest at two localities in northern Peru: (1) at 1890 m in the Rio Mayo drainage below Abra Patricia, Dpto. San Martín; (2) at 1950–1980 m east of La Peca on Cordillera Colán, Dpto. Amazonas (Fig. 2).

SPECIMENS EXAMINED.—G. flavirostris: (FMNH) 1♀, 1♂ El Carmen, Dpto. Nariño, Colombia; (LSUMZ) 2♂♂, 3♀♀ Afluente-Abra Patricia, Dpto. San Martín, Peru; (LSUMZ) 3♂♂, 2♀♀ Cordillera Azul, Dpto. Loreto, Peru; (FMNH) 1♂ Oresmapno, Dpto. Junín, Peru; (LSUMZ) 1♂, 1♀, 1 unsexed, Bosque Aputinye, Dpto. Cuzco, Peru; (LSUMZ) 1♂ Alto Palmar, Dpto. Cochabamba, Bolivia. G. ferrugineippictus: (LSUMZ) 1♀ 33 km SW Huancabamba, Dpto. Piura, Peru; (LSUMZ) 7♂♂, 3♀♀ La Peca-Cordillera Colán, Dpto. Amazonas, Peru; (LSUMZ) 2♂♂, 1 unsexed 33 km NE Ingenio, Dpto. Amazonas, Peru; (LSUMZ) 6♂♂, 1♀ Cumpang-Mashua, Dpto. La Libertad, Peru; (LSUMZ) 8♂♂, 14♀♀, (FMNH) 1♀ Cordillera Carpish, Dpto. Huancouco, Peru. G. nanus: (FMNH) 1♂ Cerro Munchique, Dpto. Cauca, Colombia; (FMNH) 1♀ Florente, Dpto. Nariño, Colombia; (LSUMZ) 4♂♂, 3♀♀ Corro Chinguela, Dpto. Piura-Cajamarca, Peru. G. loricata: (FMNH) 1♂, 1♀ (AMNH) 1♂, 1♀ La Cumbre de Valencia, Venezuela. G. peruviana: (AMNH) 1♂ (type) Chaupe, Dpto. Cajamarca, Peru; (LSUMZ) 2♂♂, 3♀♀, Playon-Lucuma on Sapalache-Carmen Trail, Dpto. Cajamarca, Peru. G. lineifrons: (AMNH) 1♀ (type) Oyacachi, Ecuador. G. ochracei-
Fig. 2. Distribution of highlands (stippled) exceeding 2000 m elev. along the lower Rio Marañón in northern Peru. The known elevational ranges of sympatric *Grallaricula* species at localities A, B, and C are: (A) Playon-Cerro Chinguela, Dpto. Cajamarca, *peruviana*—1680–2130 m, *nana*—2590–2900 m; (B) La Peca-Cordillera Colán, Dpto. Amazonas, *ochraceifrons*—1950–1980 m, *ferrugineiceps*—1890–2900 m; and (C) Afluente-Abra Patricia, Dpto. San Martín, *flavirrostris*—1070–1680 m, *ochraceifrons*—1890 m.

**REMARKS.**—Dorsally, the female is slightly darker than the male, with only a suggestion of the brightly colored forecrown (see frontispiece). The white belly and undertail coverts are lightly tinted with buff. The eye ring is incomplete with a few ochraceous buff feathers near the corners of the eye.

All the *ochraceifrons* specimens appear to be in adult plumage (18 July–30 August). The two specimens from Cordillera Colán are distinctly buffy on the lower belly and undertail coverts. Whether this is due to individual variation or subspecific difference is not known.

**ETYMOLOGY.**—The specific epithet and English name refer to the ochraceous buff forecrown of the male.

**NATURAL HISTORY NOTES**

*Grallaricula ochraceifrons* was first netted in dense undergrowth of epiphyte-laden, stunted cloud forest at 1890 m elev. on the eastern slope of the Eastern Cordillera of the Andes, Dpto. San Martín (see O’Neill and Graves 1977). In 1978, T. S. Schulenberg (18 July) and G. L. Graham (17 August) each collected a male *ochraceifrons* in the understory of tall, humid, cloud forest (canopy ca. 25 m) on the western slope of Cordillera Colán, Dpto. Amazonas. As in other species of *Grallaricula*, the new
species is quite difficult to observe in the field. The vocalizations of other Peruvian *Grallarica* (e.g., Slate-crowned Antpitta [*G. nana*], Ochre-breasted Antpitta [*G. flavirostris*], Rusty-breasted Antpitta [*G. ferrugineiceps*]) are easily recognized; however, the songs and call notes of *ochraceifrons* are unknown to us despite intensive efforts to identify and record them. The fact that no specimens were mist-netted on Cordillera Colán (up to 30 nets were set daily near areas where the two specimens were collected) suggests that this species may well be uncommon or rare. In all, this antpitta was seen only twice during 23 days of fieldwork (approx. 80 observer h) in the above localities. None of the specimens had enlarged gonads. It is interesting to note that *ochraceifrons* was syntopic with the more common and slightly smaller *ferrugineiceps* on Cordillera Colán (Table 1). We know of no other locality in Peru where two species of *Grallarica* occur in the same place. In San Martín, *flavirostris* was fairly common just below the elevational range of *ochraceifrons* (see Fig. 2).

The systematic relationships of *ochraceifrons* are obscure, but similarities in plumage and elevation of collecting stations combined with their known allopatric distributions, indicate that *ochraceifrons* and the Peruvian Antpitta (*G. peruviana*) are closely related, perhaps superspecifically. *G. peruviana* is apparently restricted to the watershed of the Rio Chinchipe, a tributary of the Rio Marañón some 120 km northwest of Cordillera Colán. A similar pattern of allopatric replacement across the lower Rio Marañón occurs in several other forest genera (e.g., *Coeligena, Metallura, Schizoeaca, Thripadectes, Grallaria, Leptopogon, Iridosornis*). In certain plumage characters, *ochraceifrons* superficially resembles the Crescent-faced Antpitta (*G. lineifrons*) of Ecuador and Colombia, and the Scallop-breasted Antpitta (*G. loricata*) of Venezuela, but pending additional information on vocalizations, which may be of primary importance in species recognition in antpittas, we hesitate to speculate further on the systematic relationships of *ochraceifrons*.

ACKNOWLEDGMENTS

We sincerely thank L. J. Barkley, M. B. Braun, J. W. Eley, G. L. Graham, D. R. Hunter, M. Sanchez, T. S. Schulenberg, R. D. Semba, K. Wehr, and M. D. Williams for hard work and sheer endurance on a series of expeditions to northern Peru which provided comparative material for this description.

Our fieldwork was generously supported by John S. Mcllhenny, E. W. Mudge, Babette M. Odum, H. Irving Schweppe, Laura R. Schweppe, and the LSUMZ. Arturo Koenig, Helen Koenig, Manuel Plenge, Isabel Plenge, and Gustavo del Solar provided much appreciated support in Lima and Chiclayo. We thank the curators of the Field Museum of Natural History (FMNH) and the American Museum of Natural History (AMNH) for the loan of specimens. Graves and Parker were able to examine type specimens while supported by Frank M. Chapman Memorial Grants. We thank K. C. Parkes, J. V. Remsen, T. S. Schulenberg, and
<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Wing chord (mm)</th>
<th>Tail (mm)</th>
<th>Tarsus (mm)</th>
<th>Culmen from base (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. ochraceifrons</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4♂♂</td>
<td>73.2–75.3 (73.2)</td>
<td>31.7–33.5 (32.6)</td>
<td>24.8–26.7 (25.9)</td>
<td>16.7–17.3 (17.1)</td>
<td>22.5–23.8 (23.1)</td>
</tr>
<tr>
<td></td>
<td>1♀</td>
<td>71.2</td>
<td>31.9</td>
<td>27.0</td>
<td>16.9</td>
<td>—</td>
</tr>
<tr>
<td><em>G. flavirostris</em>&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2♂♂</td>
<td>63.3–65.7 (64.5)</td>
<td>26.3–27.6 (27.0)</td>
<td>21.9–23.0 (22.5)</td>
<td>15.1–16.3 (15.7)</td>
<td>14.5–15.2 (14.9)</td>
</tr>
<tr>
<td></td>
<td>3♀♀</td>
<td>63.0–64.2 (63.4)</td>
<td>24.4–27.4 (26.0)</td>
<td>22.3–24.4 (23.3)</td>
<td>15.4–16.1 (15.7)</td>
<td>15.6–17.7 (16.8)</td>
</tr>
<tr>
<td><em>G. ferrugineicuclus</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>7♂♂</td>
<td>69.5–74.9 (72.0)</td>
<td>38.0–41.6 (39.9)</td>
<td>25.0–27.2 (26.2)</td>
<td>15.4–17.5 (16.7)</td>
<td>15.5–18.5 (16.6)</td>
</tr>
<tr>
<td></td>
<td>3♀♀</td>
<td>66.8–68.4 (67.7)</td>
<td>36.1–38.6 (37.6)</td>
<td>25.9–26.4 (26.2)</td>
<td>15.5–16.1 (15.9)</td>
<td>16.5–17.0 (16.7)</td>
</tr>
<tr>
<td><em>G. peruviana</em>&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2♂♂</td>
<td>70.0–70.8 (70.4)</td>
<td>30.6–30.7 (30.7)</td>
<td>23.5–24.0 (23.8)</td>
<td>16.6 (16.6)</td>
<td>17.0–17.5 (17.3)</td>
</tr>
<tr>
<td></td>
<td>3♀♀</td>
<td>69.6–71.5 (70.6)</td>
<td>31.1–31.6 (31.4)</td>
<td>23.7–24.5 (24.2)</td>
<td>15.8–16.6 (16.3)</td>
<td>19.5–21.0 (20.2)</td>
</tr>
</tbody>
</table>

<sup>a</sup> Abra Patricia, La Peca-Cordillera Colán, Dpto. San Martín and Amazonas.
<sup>b</sup> Affluente-Abra Patricia, Dpto. San Martín.
<sup>c</sup> La Peca-Cordillera Colán, Dpto. Amazonas.
<sup>d</sup> Playon-Cerro Chinguela, Dpto. Cajamarca.
M. D. Williams for helpful comments. The Direcccion General Forestal y de Fauna of the Ministerio de Agricultura, Lima, Peru, provided permits and supported our research.

LITERATURE CITED


COLOR PLATE

The colorplate Frontispiece of the Ochre-fronted Antpitta (Grallaricula ochraceifrons) has been made possible by an endowment by the late George Miksch Sutton. Painting by John P. O'Neill.
COWBIRD PARASITISM OF DICKCISSELS IN DIFFERENT HABITATS AND AT DIFFERENT NEST DENSITIES

JOHN L. ZIMMERMAN

When bison (*Bison bison*) grazed the plains, the Brown-headed Cowbird (*Molothrus ater*) lived in commensal association with it (Hamilton and Orians 1965); the lack of territoriality, promiscuous mating system (Elliott 1980), and nest parasitism characteristic of the cowbird are possible adaptations to the nomadic patterns of these large herbivores (Hill 1976). *B. bison* are no longer free-roaming on the prairie and cowbirds have expanded their range with the replacement of the eastern deciduous forest by agronomic communities (Friedmann 1929). They have exploited new hosts (Mayfield 1965) and developed more sedentary behavior patterns (Laskey 1950; Darley 1978, 1982), perhaps in response to the greater availability of host species in the east (Dufty 1982).

In the plains, however, the cowbird has retained its less site-specific behavior and still shows a preference for the “prairie shrub succession” (Lowther and Johnston 1977), those seral communities that would develop in the wake of severe use by large herds of grazers. The Dickcissel (*Spiza americana*) is also adapted to these successional communities (Zimmerman 1971) and to prairie in which herbivore grazing increases forb diversity (Herbel and Anderson 1959), even though suitable nest-sites are fewer (Zimmerman 1982).

As inhabitants of the same communities for so long, the Dickcissel should have evolved to ameliorate the impact of social parasitism on its productivity (Gochfeld 1979). Although the incidence of parasitism is low in peripheral parts of the Dickcissel’s current range (Harmeson 1974, Goertz 1977), in the areas of highest densities, the percent of Dickcissel nests parasitized by the cowbird ranges from 31–33% in oldfield habitats (Overmire 1962, Wiens 1963) to 50–53% (Hergenrader 1962, Hill 1976) and even 95% in grazed prairie (Elliott 1978).

Fretwell (1977) has suggested that the introduction of domestic grain crops into the llanos of northern South America at the expense of small-seeded native plants is responsible for the demonstrated difference in survival between male and female Dickcissels during the non-breeding season. The smaller females have experienced a reduction in food availability with the conversion of natural habitats into croplands and have suffered higher mortality so that fewer females return north in the spring. Given the higher incidence of cowbird parasitism in habitats where Dick-
cissels are less abundant, Fretwell (1977) has hypothesized an inverse relationship between host nest density and the intensity of cowbird parasitism. Assuming cowbird parasitism has a depressing effect on host productivity (although this is not always the case, Smith 1981), he further suggested that the increasing impact of cowbird parasitism with decreasing Dickcissel nest density will be the final factor that drives the Dickcissel to extinction once female densities have been sufficiently reduced by the size-related mortality on the wintering range.

The purposes of this paper are: (1) to determine the severity of the impact of the high frequency of cowbird nest parasitism on Dickcissel productivity, (2) analyze the incidence and intensity of parasitism as a function of habitat and the density of host nests, and (3) to assess the productivity of cowbirds in Dickcissel nests.

METHODS

Nest data were obtained from 1965–1979 in oldfield populations on the Ft. Riley Military Reservation and in grasslands on the Konza Prairie Research Natural Area in Riley and Geary counties, Kansas. The two separate oldfield sites were 25.5 km and 12.0 km from the prairie sites. Indeed, the closer oldfield was in sight from the highest ridges on the prairie.

Except for a few populations where nests were visited every 3 or 4 days, most data were gathered by weekly visits to the nests. Week of initiation was known for many nests, but estimated for the majority. For nestlings expected to fledge between visits, the fate of the nests was determined by the female’s behavior. At successful nests the female remained in the immediate area feeding the young and giving aggressive displays to my presence. If a nest was lost since the last visit, the female was always gone. The number of fledglings was the number of nestlings at the last visit. Clutch-size data were based on nests assumed to have complete clutches, while all nests found were used to determine the frequency of parasitism and egg success percentages, even though some of these nests failed before egg-laying had been completed. Nesting success data are also presented as survival rates (Mayfield 1961, 1975) with the 95% confidence limits calculated by Johnson’s (1979) method.

For three oldfield populations studied in three different years on two plots of 22.7 ha and 30.4 ha and two prairie populations on plots of 28.8 ha and 12.2 ha, concurrent investigations of territoriality and mating patterns provided an intensity of coverage that makes me confident that most nests were found. For these populations, therefore, it was possible to relate the intensity of cowbird parasitism with the density of available nests as well as determine the production of cowbirds per unit area according to habitat. As observed elsewhere in the Great Plains, cowbird egg-laying decreases markedly in July (Wiens 1963, Newman 1970, Hill 1976, Payne 1976) when Dickcissel densities reach their maximum. To compensate for the assumed physiologically-based decline in cowbird egg deposition before that of the Dickcissel, the density analysis was conducted for all weeks up to the week that the density of cowbird eggs/ha fell below 50% of the previous week’s average. Since only 1.3% of all cowbird eggs laid in prairie nests and only 2.4% of all those in oldfield nests were deposited after the egg-laying period of the host, the density of available nests was determined on just those nests that were under construction or receiving host eggs, those being incubated or brooded were excluded. Nests under construction were included in density calculations for that week as well as in the proportion of nests parasitized even though they might not have received
Zimmerman · DICKCISSELS AND COWBIRDS

Table 1
MEAN (±SE) COWBIRD EGGS PER PARASITIZED NEST (N)\(^a\) AND PERCENT NESTS PARASITIZED (N)\(^a\) ACCORDING TO WEEK OF NEST START AND HABITAT

<table>
<thead>
<tr>
<th>Dates</th>
<th>Oldfield Cowbird eggs</th>
<th>% parasitized</th>
<th>Prairie Cowbird eggs</th>
<th>% parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>18–24 May</td>
<td>7.0 (1)(^a)</td>
<td>100 (2)(^b)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>25–31 May</td>
<td>1.9 ± 0.26 (17)</td>
<td>90 (21)</td>
<td>3.2 ± 0.95 (4)(^a)</td>
<td>100 (4)(^b)</td>
</tr>
<tr>
<td>1–7 June</td>
<td>2.7 ± 0.31 (25)</td>
<td>83 (36)</td>
<td>3.7 ± 0.56 (11)</td>
<td>100 (12)</td>
</tr>
<tr>
<td>8–14 June</td>
<td>2.6 ± 0.27 (31)</td>
<td>71 (54)</td>
<td>3.0 ± 0.63 (8)</td>
<td>89 (9)</td>
</tr>
<tr>
<td>15–21 June</td>
<td>2.1 ± 0.24 (31)</td>
<td>57 (58)</td>
<td>3.0 ± 0.36 (24)</td>
<td>93 (29)</td>
</tr>
<tr>
<td>22–28 June</td>
<td>2.2 ± 0.28 (25)</td>
<td>65 (48)</td>
<td>3.2 ± 0.41 (16)</td>
<td>91 (22)</td>
</tr>
<tr>
<td>29–5 July</td>
<td>2.3 ± 0.26 (36)</td>
<td>72 (54)</td>
<td>2.7 ± 0.35 (16)</td>
<td>79 (24)</td>
</tr>
<tr>
<td>6–12 July</td>
<td>2.5 ± 0.26 (21)</td>
<td>60 (35)</td>
<td>2.4 ± 0.37 (10)</td>
<td>83 (12)</td>
</tr>
<tr>
<td>13–19 July</td>
<td>1.9 ± 0.31 (10)</td>
<td>27 (44)</td>
<td>2.0 ± 0.55 (5)</td>
<td>67 (9)</td>
</tr>
<tr>
<td>20–26 July</td>
<td>2.5 ± 0.64 (4)</td>
<td>21 (19)</td>
<td>2.0 ± 0.0 (2)</td>
<td>0 (3)</td>
</tr>
<tr>
<td>27–2 Aug.</td>
<td>—</td>
<td>14 (7)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>3–9 Aug.</td>
<td>—</td>
<td>0 (6)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>10–16 Aug.</td>
<td>—</td>
<td>0 (1)</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

\(^a\) N for cowbird eggs based on nests with complete clutches.
\(^b\) N for percent parasitism based on all nests found.

any cowbird eggs until the following week, since nest-building behavior may be an important location cue for the cowbird (Norman and Robertson 1975).

HABITAT DIFFERENCES

Of 385 Dickcissel nests in oldfields, 60.0% were parasitized, while 84.8% of 235 prairie nests were parasitized. This difference is significant (\(\chi^2 = 7.67, \text{df} = 1, P < 0.05\)). On a weekly basis, the percent of nests parasitized dropped off earlier in oldfields, finally falling below 50% the week of 13–19 July. In the prairie, the level of parasitism remained higher longer, but similarly fell below 50% after the middle of July (Table 1).

The mean number of cowbird eggs per parasitized nest was also greater in the prairie (Table 1), with weekly means being significantly larger in the prairie during 25–31 May (\(t = 2.01, \text{df} = 19, P < 0.05\)), 1–7 June (\(t = 1.69, \text{df} = 34, P < 0.05\)), and 22–28 June (\(t = 2.08, \text{df} = 39, P < 0.05\)). This difference was also reflected in the larger proportion of multiple cowbird egg clutches in prairies (Fig. 1). While there was no change in the mean number of cowbird eggs in oldfield nests during the nesting season, the mean number laid in prairie nests did significantly decrease with time (\(b = -0.194, t = 5.51, \text{df} = 7, P < 0.01\)), paralleling the drop in the frequency of parasitism.
Since parasitized prairie nests had an increased total clutch-size, incubation times could have been increased due to the inability of the female to maintain an adequately high egg temperature over all the eggs or the need for the female to be off the nest for longer inattentive periods of feeding in response to increased energy demands (Biebach 1981). This would then increase the time the nest would be exposed to predation, decreasing the survival rates of prairie nests. Incubation time (Table 2) was prolonged in larger clutches (Spearman $R = 0.68$, $N = 7$, $P < 0.06$). But the lengthened incubation period or the increased nest contents had no effect on the daily survival rates of nests since there were no differences according to clutch- and/or brood-size (Table 3).

Some nests were lost by the females’ desertion when all host eggs had been removed by cowbirds or when clutch-size became too large, but there was no difference between habitats. Only 8.7% of all prairie nests were abandoned in response to cowbirds (73% of the time this was during the egg-laying period, while the rest were early in incubation). A similar proportion (8.8%) of prairie nests was also abandoned for reasons other than an assumed interference by cowbirds. Among parasitized nests this type of abandonment comprised 6.6% of the total number of nests, while among non-parasitized nests 21.0% were abandoned. In the oldfield, 9.1% of the nests were deserted due to cowbird interference with the majority of these (83%) being abandoned during the egg-laying period. Only 3.6% of the oldfield nests were abandoned for reasons not attributable to cow-

---

**Table 2**

<table>
<thead>
<tr>
<th>Eggs in clutch</th>
<th>Mean days of incubation</th>
<th>No. eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>12.3 ± 0.33</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>12.0 ± 0.44</td>
<td>22</td>
</tr>
<tr>
<td>5</td>
<td>12.0 ± 0.17</td>
<td>15</td>
</tr>
<tr>
<td>6</td>
<td>11.5 ± 0.20</td>
<td>34</td>
</tr>
<tr>
<td>7</td>
<td>12.4 ± 0.22</td>
<td>10</td>
</tr>
<tr>
<td>8</td>
<td>13.2 ± 0.17</td>
<td>6</td>
</tr>
<tr>
<td>10</td>
<td>13.7 ± 0.21</td>
<td>6</td>
</tr>
</tbody>
</table>

a In days, beginning the day the last egg was laid.

b All eggs, including cowbird eggs in parasitized nests.

---

**Fig. 1.** Percent frequency distribution of cowbird eggs per nest in oldfield (cross-hatched) and prairie (open) habitats. Number at top of each bar is the total number of nests with that cowbird clutch in each habitat.
Table 3
Clutch- and/or Brood-size\(^a\) vs Daily Survival Rate ± 95% Confidence Limits (No. Nests)

<table>
<thead>
<tr>
<th>Clutch- or brood-size</th>
<th>Oldfield</th>
<th>Prairie</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.91 ± 0.10 (4)</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>0.89 ± 0.07 (10)</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>0.91 ± 0.03 (46)</td>
<td>0.97 ± 0.04 (6)</td>
</tr>
<tr>
<td>4</td>
<td>0.94 ± 0.01 (110)</td>
<td>0.96 ± 0.03 (22)</td>
</tr>
<tr>
<td>5</td>
<td>0.94 ± 0.02 (67)</td>
<td>0.93 ± 0.03 (25)</td>
</tr>
<tr>
<td>6</td>
<td>0.96 ± 0.02 (48)</td>
<td>0.94 ± 0.03 (20)</td>
</tr>
<tr>
<td>7</td>
<td>0.96 ± 0.02 (17)</td>
<td>0.95 ± 0.03 (18)</td>
</tr>
<tr>
<td>8</td>
<td>0.92 ± 0.05 (11)</td>
<td>0.93 ± 0.05 (10)</td>
</tr>
<tr>
<td>9-15</td>
<td>0.94 ± 0.03 (17)</td>
<td>0.95 ± 0.04 (12)</td>
</tr>
</tbody>
</table>

\(^a\) Mixed broods of cowbirds and Dickcissels corrected to equal biomass, 1 cowbird young = 1.3 Dickcissel young (Hatch 1975).

birds. Among oldfield parasitized nests, 4.3% were deserted in this way, while 2.6% of non-parasitized nests failed because of abandonment. The proportions of nest desertions as a result of cowbird disturbances in both oldfield and prairie habitats are less than those in "common fosterers" affected by the European Cuckoo (Cuculus canorus) (Jourdain 1925:651), as well as lower than observed for the Yellow Warbler (Dendroica petechia) (Clark and Robertson 1981) or in the prairie species studied by Elliott (1978). Smith (1981), however, concluded that there was no evidence to attribute nest desertion by Song Sparrows (Melospiza melodia) in his population to cowbird activity.

EGG REMOVAL BY COWBIRDS

The frequency distribution of completed clutch-sizes for Dickcissel eggs in both parasitized and non-parasitized nests is illustrated in Fig. 2. The assumption that this difference is due to the removal of eggs by the cowbird from parasitized nests is supported by a single observation of a female cowbird leaving a nest with a Dickcissel egg. There are no significant differences between oldfield and prairie habitats in the mean clutch-sizes of non-parasitized or parasitized nests (Zimmerman 1982); thus, data from both habitats have been combined to estimate the numbers of Dickcissel eggs removed per nest by the cowbird (Fig. 3).
PERCENT

PARASITIZED

\[ \bar{X} = 2.4 \]

NON-PARASITIZED

\[ \bar{X} = 4.0 \]
The mean completed clutch-size in non-parasitized nests significantly decreased with nest-starting date \((b = -0.073, \ t = 2.63, \ df = 147, \ P < 0.01)\), but there was no temporal change in the numbers of Dickcissel eggs in parasitized nests \((\bar{x} = 2.4, \ SE = \pm 0.06, \ N = 297)\). Egg removal was estimated on a weekly basis by subtracting the parasitized clutch-size mean for each week from the corresponding mean for non-parasitized nests. This difference is plotted in Fig. 3, and there is also a significant regression with time of nest start \((b = -0.118, \ t = 4.176, \ df = 7, \ P < 0.01)\). Thus, early in the nesting season (late May and June), there were about two Dickcissel eggs removed by cowbirds from each parasitized nest, but this loss decreases to close to one egg per nest by late July. The
median value across all weeks is 1.65 eggs. This is a greater loss than suffered by the American Goldfinch (*Carduelis tristis*) (Middleton 1977), Prairie Warbler (*Dendroica discolor*) (Nolan 1978) or Song Sparrow (Nice 1937), less heavily parasitized hosts inhabiting geographic areas more recently invaded by the cowbird, and closer to Elliott’s (1978) estimates based on hatchling counts rather than completed clutches for the Dickcissel, Grasshopper Sparrow (*Ammodramus savannarum*), and Eastern Meadowlark (*Sturnella magna*) in Kansas grazed prairie.

**IMPACT ON PRODUCTIVITY**

While the survival rates of Dickcissel nests were not greatly affected by cowbird parasitism, the production of Dickcissels was depressed by the removal of host eggs by the cowbird (Table 4). In oldfields there was a significant difference in the mean number of Dickcissels fledged per successful non-parasitized nest and the number fledged per successful parasitized nest ($t = 5.76$, df = 109, $P < 0.01$). Similarly, in prairies the number fledged per successful non-parasitized nest was significantly different from the mean number fledged from successful parasitized nests ($t = 4.40$, df = 48, $P < 0.01$). In both habitats there were no significant differences between total young (including cowbirds in parasitized nests) fledged per successful nest when parasitized and non-parasitized were compared. There appears to be a definite (optimum?) number of young (about 3.5) the female can rear (males take no part in parental care, Zimmerman 1966), no matter what the habitat and no matter if some of the young in the brood are cowbirds. Not surprisingly this value is similar to the unparasitized clutch-size of four (Zimmerman 1982).

Table 4 also presents the egg success rates for Dickcissels in oldfield and prairie habitats. The lower fledging success of both Dickcissel and cowbird eggs in oldfields resulted from significantly higher predation rates during incubation compared to the prairie (Zimmerman, unpubl.). The reduction in recruitment calculated according to Payne’s (1977) method is 26.9% in oldfields and 29.1% in prairies, values exceeded in Payne’s analysis by only the Red-eyed Vireo (*Vireo olivaceous*), a relatively newer host of the eastern deciduous forest. While these two values are not significantly different, their magnitudes do correspond with the habitat differences in the frequency and intensity of cowbird parasitism.

Using the numbers of eggs remaining in parasitized clutches after the removal of host eggs by the cowbird (246 in prairie nests and 513 in oldfield nests), a comparison with egg success in unparasitized nests might indicate detrimental interaction of Dickcissel and cowbird nestlings. For oldfields, 23.0% of the eggs remaining in parasitized nests fledged. If eggs
lost to abandonment in response to cowbird disturbance are accounted for, this value is 24%. Neither of these values is significantly different from the 30.9% egg success rate in unparasitized oldfield nests. In the case of prairie nests, however, only 30.9% of the host eggs remaining fledged and this value is significantly different from the 52.4% egg success in unparasitized prairie nests ($\chi^2 = 8.83$, df = 1, $P < 0.01$). When eggs lost to cowbird induced abandonment are accounted for, the resulting 32.7% success rate is still significantly different ($\chi^2 = 6.99$, df = 1, $P < 0.01$).

When the fates of the remaining eggs in prairie nests that did not produce fledglings were compared between parasitized and non-parasitized clutches, predation losses (60 vs 64%), and eggs that did not hatch (17 vs 20%) were similar. Abandonment for unknown reasons and loss of nests from violent weather accounted for 17% of the remaining eggs in unparasitized nests, but only 4% of the eggs in parasitized nests. Unexplained disappearances of eggs and nestlings, on the other hand, were the fate of 12% of the unsuccessful eggs in parasitized nests, while only the cause of 6% of the loss in unparasitized clutches. It does not seem, however, that cowbird parasitism is clearly responsible for the lower success of the eggs remaining after egg removal by cowbirds in parasitized nests. There was
no difference in incubation times between cowbird and Dickcissel eggs that would adversely affect later hatching young. The mean incubation time for 30 cowbird eggs was 12.1 days (SE = ±0.22) and were 12.0 days (SE = ±0.18) for 66 Dickcissel eggs. Hatch (1975) measured growth rates of host young and cowbird young in Dickcissel nests and found no detrimental effect on the growth rate of Dickcissels when compared to their growth rate in unparasitized nests.

**COWBIRD PRODUCTIVITY**

Scott and Ankney (1980) generalized a fledging success of 15% for cowbird eggs. This is very close to the actual data compiled for oldfield Dickcissel nests in my study (Table 4). The fledging success of cowbird eggs laid in prairie nests was greater and significantly different from the oldfield value ($\chi^2 = 5.25, df = 1, P < 0.05$). This higher probability of a cowbird egg laid in a prairie Dickcissel nest of producing a fledgling, coupled with the greater number of cowbird eggs per prairie nest, resulted in the fledging of 0.65 cowbirds per parasitized nest (SE = ±0.10, $N = 106$) in the prairie, almost twice as great as the 0.37 cowbirds fledged per parasitized oldfield nest (SE = ±0.05, $N = 230$). But this higher production of cowbirds per prairie nest is offset by the lower density of host nests. For the prairie populations in which the number of nests found were thought to be quite close to the number actually present, the production of cowbirds was 0.32 fledglings per ha (total area = 41.0 ha). Because of higher nest densities in the oldfield populations, cowbird production was 0.54 fledglings per ha (total area = 75.8 ha). In these oldfields there were only a few Red-winged Blackbirds (*Agelaius phoeniceus*) to serve as alternate hosts in one field and no alternate hosts in the other two fields. In prairies, on the other hand, the availability of alternate hosts is greater (Elliott 1978). But without the nest density values for these alternate hosts it is not possible to compare the suitabilities of the two habitats for the cowbird.

**EFFECT OF NEST DENSITY**

As was expected, there was a lack of synchrony between the breeding activity of the cowbird and that of the Dickcissel in three oldfield and two prairie populations in which the number of known nests was thought to closely approximate the number actually present (Fig. 4). On the basis of the methods previously described, 26 weekly Dickcissel nest-density values were available from the 43 densities displayed in Fig. 4 and were used to test Fretwell’s (1977) hypothesis that the intensity of cowbird parasitism is inversely related to the density of host nests. These weekly nest-
Fig. 4. Dickcissel nest density (closed circles) and cowbird egg density (open circles) in three oldfield and two prairie populations by week over the period of cowbird parasitism.

density values were analyzed with both the percent of nests newly parasitized that week and with McGeen’s (1972) “cowbird pressure,” defined as the product of the percent of parasitism and the frequency of nests with more than one cowbird egg (Table 5).
### Table 5

**Weekly Nest Densities in Oldfields and Prairies, and Cowbird Parasitism**

<table>
<thead>
<tr>
<th>Available nests/ha (N)</th>
<th>% parasitized</th>
<th>% multiple cowbird eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.03 (1)</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>0.04 (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.04 (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.04 (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.07 (2)</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>0.07 (2)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.08 (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.08 (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.09 (2)</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>0.13 (3)</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>0.14 (4)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>0.14 (4)</td>
<td>75</td>
<td>100</td>
</tr>
<tr>
<td>0.16 (2)</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>0.20 (6)</td>
<td>50</td>
<td>67</td>
</tr>
<tr>
<td>0.21 (6)</td>
<td>83</td>
<td>80</td>
</tr>
<tr>
<td>0.25 (3)</td>
<td>33</td>
<td>0</td>
</tr>
<tr>
<td>0.30 (9)</td>
<td>44</td>
<td>75</td>
</tr>
<tr>
<td>0.43 (13)</td>
<td>77</td>
<td>50</td>
</tr>
<tr>
<td>0.46 (14)</td>
<td>79</td>
<td>18</td>
</tr>
<tr>
<td>0.46 (14)</td>
<td>43</td>
<td>67</td>
</tr>
<tr>
<td>0.53 (16)</td>
<td>75</td>
<td>50</td>
</tr>
<tr>
<td>0.53 (16)</td>
<td>69</td>
<td>36</td>
</tr>
<tr>
<td>0.57 (13)</td>
<td>85</td>
<td>82</td>
</tr>
<tr>
<td>0.62 (14)</td>
<td>36</td>
<td>40</td>
</tr>
<tr>
<td>0.75 (17)</td>
<td>29</td>
<td>40</td>
</tr>
</tbody>
</table>

Both the frequency of cowbird parasitism and McGeen's (1972) cowbird pressure are significantly and inversely associated with the density of available nests (Spearman $R = -0.774$, $N = 26$, $P < 0.01$ for frequency; Spearman $R = -0.837$, $N = 22$, $P < 0.01$ for pressure). These values were calculated from data from both habitats, but evaluation of each habitat separately also demonstrated a significant inverse relationship. Fretwell's (1977) hypothesis that the Dickcissel will suffer heavy cowbird parasitism when nesting densities are reduced is supported by these results. If it is assumed that all other factors affecting Dickcissel recruitment remain at the same level of intensity, then it is perhaps conceivable that extinction of the species might ensue as Fretwell predicts. But predation is still the major cause of nest loss in Dickcissels, and its impact is positively associated with nest density (Fretwell 1977). With lowering nest
densities preda
tion pressure should abate and mitigate the rate of popu-
lation decline, perhaps permitting regulation at a new, but lower, popu-
lation level that can be subsequently maintained.

This relationship between nest density and cowbird parasitism also ex-
plains the difference in the frequency and intensity of cowbird parasitism
between habitats. Nest densities are much lower in prairies than in old-
fields due to the greater number of males and the higher incidence of polygyny in oldfield populations (Zimmerman 1971).

SUMMARY

Nest histories from Dickcissel populations in oldfields and prairies of Kansas were analyzed to ascertain the impact of cowbird parasitism on Dickcissel productivity, assess the product-
tivity of Brown-headed Cowbirds in Dickcissel nests, and test Fretwell’s (1977) hypothesis that the frequency and intensity of cowbird parasitism were inversely related to host nest density.

Both the frequency and the intensity of cowbird parasitism were significantly greater in prairie populations than in oldfield populations of the Dickcissel. The fledging success of the greater number of cowbird eggs laid per prairie nest was also higher so that almost twice as many cowbirds were fledged from each parasitized prairie nest than were produced from each parasitized oldfield nest.

In both habitats less than 10% of the nests were abandoned in response to cowbird activity. The major effect of parasitism on Dickcissel productivity was the removal of host eggs by the cowbird that resulted in a significant reduction in the numbers of Dickcissels fledged from parasitized nests in both habitats. Early in the nesting season, almost two eggs were removed from each parasitized nest, but this loss decreased to about one egg by mid-July. The reduction in recruitment (Payne 1977) is 26.9% in oldfields and 29.1% in prairies.

Both the frequency of cowbird parasitism and intensity as measured by the “cowbird pressure” (McGeen 1972) were inversely associated with the density of available nests, supporting Fretwell’s (1977) hypothesis. This relationship also explains the habitat difference in parasitism since Dickcissel densities were lower in the prairie.

ACKNOWLEDGMENTS

This work was funded by grant GB–6087 from the National Science Foundation and NSF Undergraduate Research Participation programs during several successive summers as well as from support provided by the Chapman Memorial Fund of the American Museum of Natural History. Permission to conduct this work on the selected study sites was generously granted by the Commander, Headquarters Fort Riley, and the Director of the Konza Prairies Research Natural Area. Such an extensive sample of nest records could never have been accumulated without the diligent efforts of Gil Blankespoor, Jeff Fergen, Elmer Finck, Scott Hatch, Harvard Townsend, and Steve Wiegert. The conscientious critiques by Steve Rothstein and D. M. Scott greatly improved the submitted draft of this paper.

LITERATURE CITED


Clark, K. L. and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-


DIV. BIOLOGY, KANSAS STATE UNIV., MANHATTAN, KANSAS 66506. ACCEPTED 5 AUG. 1982.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in memory of Aaron M. Bagg, a former president of the society. The Student Membership Committee has made the awards for the 1982 applicants and the following students have been given student memberships for 1983 in the Wilson Ornithological Society: Steven R. Beissinger, University of Michigan; Theodore Thomas Buerger, Auburn University; Ann Marie Francis, University of Wisconsin; R. Given Harper, Western Illinois University; Bradley G. Hill, University of Calgary; Lee Richard Jones, Utah State University; Kimberly Dawn Kyker, University of Oklahoma; Brian Alan Maurer, University of Arizona; J. Michael Reed, University of Montana; Dan Alan Roberts, University of North Carolina (Charlotte); Mark Alan Shields, University of North Carolina (Wilmington); Steven Charles Sibley, Mississippi State University; Douglas William White, Rutgers University; Ann M. Wyckoff, University of North Dakota.

EFFECTS OF INVESTIGATOR ACTIVITY ON RING-BILLED GULL BEHAVIOR AND REPRODUCTIVE PERFORMANCE

PETER M. FETTEROLF

Human disturbance can be a detriment to hatching success in Herring Gulls (Larus argentatus) (Hunt 1972) and Western Gulls (L. occidentalis) (Robert and Ralph 1975). The activities of scientists can also cause significant reductions in fledging success (Glaucous-winged Gull [L. glaucescens]) (Gillett et al. 1975). These studies and others (Emlen 1956, Tinbergen 1960, Ashmole 1963, Harris 1964, Kadlec et al. 1969, Anderson and Keith 1980) have reported the behavior of chicks in response to human intrusion but none has quantified the observed behavior of adults and chicks. In this study I: (1) quantify human disturbance effects on Ring-billed Gull (L. delawarensis) adult and chick behavior, as well as reproductive performance; (2) compare past findings on reproductive performance to data I collected at two different colonies in four different years; and (3) examine the theoretical ramifications of biased reproductive performance resulting from human activity.

STUDY AREAS AND METHODS

Mugg's Island.—I collected data on gull behavior and reproductive performance on Mugg's Island, Toronto Harbour, Toronto, York RM, Ontario, Canada, from April through July 1976–1978. The colony is inhabited by about 6000 pairs of Ring-billed Gulls and 50 pairs of Herring Gulls. The site is described elsewhere (Fetterolf 1979a).

Three study plots were located 2–7 m from an observation blind on top of a hill in the eastern section of the colony (Fig. 1). Each plot measured 7 × 14 m and half of each supported only very sparse vegetation (open habitat). The other half had little or no vegetation but was cluttered with driftwood and wooden stakes (1 × 3 × 40 cm) (driftwood habitat) which I placed in the areas in late fall of 1975. The open habitat sections of plots 1 and 3 had a few emergent sandbar willows (Salix interior) (0.10–0.75 m high) growing at one end of the section.

Eastern Headland.—I gathered data on reproductive performance at 17:30 on 27 June 1980 at the Eastern Headland, Toronto Outer Harbour (for description of the site see Blokpoel and Fetterolf 1978). The sampling area (15 × 30 m) was situated amongst about 4000 Ring-billed Gull nests and was nearly devoid of vegetation. Two clumps of lamb's-quarters (Chenopodium album) and two pieces of wood delimited the sampling area.

Disturbance regimes.—The level of investigator activity in each plot at each colony is summarized for each year in Table 1. I documented the effects of investigator activity on gull behavior only in 1977 on Mugg's Island.

Nest checks prior to hatching of eggs.—To determine the number of eggs laid in each nest on Mugg's Island, my assistant and I visited each plot every second day if there was no precipitation. We marked eggs with a felt-tipped pen, staked nests with numbered tongue
Fig. 1. Map of northeastern end of Mugg's Island showing the study plots, the nesting areas of Herring (///) and Ring-billed gulls (-----), and the route (•••) taken by my assistant during experimental disturbances. Driftwood in each plot is represented by wavy lines.

depressors, and recorded time spent in each plot. On the Eastern Headland, the study area was entered only once during mid-incubation to count nests. Eggs and nests were not marked.

Observation of Investigator Activity After Onset of Hatch of Eggs, 1977

Documentation of gull behavior.—Every second day from 17 May until 3 June 1977, I documented the effects of investigator activity on gull behavior by observing from the blind while my assistant visited the moderately and most disturbed plots (plots 1 and 2, respectively; Fig. 1). I entered the observation blind at approximately 15:00 on the day prior to experimental disturbances by passing through the western edge of the moderately disturbed plot yet avoiding the other two plots. Each experimental session began at about 12:00 after I had spent the night in the blind to insure that disturbance during entry to the blind did not affect the results. For 30 min before my assistant entered the study plots, I continuously scanned all three plots to record behavior (pre-disturbance observation period).

At about 12:30 my assistant entered the colony from the southeast (Fig. 1) and checked nests in the moderately disturbed plot for hatching eggs while I recorded gull behavior (disturbance observation period). She walked
<table>
<thead>
<tr>
<th>Plot</th>
<th>Year</th>
<th>Colony</th>
<th>Visits before hatching</th>
<th>Time in plot (min)</th>
<th>Visits after hatching</th>
<th>Time in plot (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2, 3</td>
<td>1976</td>
<td>Mugg's Island</td>
<td>every 2nd day</td>
<td>15</td>
<td>every 2nd day</td>
<td>15</td>
</tr>
<tr>
<td>1 (Moderately disturbed)</td>
<td>1977</td>
<td>Mugg's Island</td>
<td>every 2nd day</td>
<td>7.8 ± 1.8&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>every 2nd day</td>
<td>8.5 ± 4.5&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>2 (Most disturbed)</td>
<td>1977</td>
<td>Mugg's Island</td>
<td>every 2nd day</td>
<td>5.8 ± 2.3&lt;sup&gt;b,d&lt;/sup&gt;</td>
<td>every 2nd day</td>
<td>22.1 ± 11.2&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>3 (Least disturbed)</td>
<td>1977</td>
<td>Mugg's Island</td>
<td>every 2nd day</td>
<td>9.3 ± 2.2&lt;sup&gt;d&lt;/sup&gt;</td>
<td>once</td>
<td>5.9</td>
</tr>
<tr>
<td>3&lt;sup&gt;e&lt;/sup&gt;</td>
<td>1978</td>
<td>Mugg's Island</td>
<td>every 2nd day</td>
<td>6.5 ± 3.3</td>
<td>not entered</td>
<td>—</td>
</tr>
<tr>
<td>—</td>
<td>1980</td>
<td>Eastern Headland</td>
<td>once</td>
<td>15</td>
<td>not entered</td>
<td>—</td>
</tr>
</tbody>
</table>

<sup>a</sup> Time in plots shown as means ± 1 SD, except where estimated.
<sup>b</sup> t = 2.44, df = 22, P < 0.05.
<sup>c</sup> t = 3.40, df = 16, P < 0.01.
<sup>d</sup> t = 4.32, df = 22, P < 0.001.
<sup>e</sup> Egg hatching in plots one and two was altered by exchanging eggs, so reproductive performance is not reported for these plots.
the perimeter of the plot, recorded the presence of newly emerged chicks and marked chicks without handling them using a weak picric acid solution sprayed from a plant mister. After checking each nest in the moderately disturbed plot, my assistant walked from the colony and I recorded behavior for 30 min in the plot (post-disturbance observation period). Following my 30 min post-disturbance watch, my assistant returned via the same route, entered the most disturbed plot and walked slowly to each nest while I recorded gull behavior (disturbance observation period). At the nest, she weighed freshly hatched chicks, banded them with expandable leg bands, and sprayed them with the picric acid solution. She then left the colony and I made a 30 min post-disturbance watch in the most and least disturbed plots. Visits were stopped when chicks in the moderately and most disturbed plots were at least a week old. The least disturbed plot was visited once after egg-pipping began (on 22 May) when my assistant and I checked hatching success in a few nests obscured by vegetation. No known human intrusions occurred in this plot after this date.

To document behavior I counted adult fights, chick runs, adult attacks on chicks, and the number of pecks delivered per attack. Behavior recorded as an adult fight included each or any combination of the following behaviors directed to another adult: (1) charging with wings outspread; (2) thrusting closed bill; and (3) grasping the bill or wing and tugging. I recorded a chick run whenever a chick walked or ran from its natal territory. Off the territory, I could not identify each individual chick because they often stopped and joined a group of young. Therefore, whenever a chick stopped running for at least 5 sec and then ran, I counted a chick run. An adult attack was recorded whenever an adult pecked or grasped and shook a chick. I counted the number of pecks in any attack and calculated the average pecks per attack (pecking rate). The reported values are probably low estimates because activity during (and often after) disturbance was so chaotic that events were likely missed.

**Documentation of chick fates.**—To measure the effects of investigator activity on the lives of chicks, I monitored the fate of chicks daily. Fates (decreases in brood-size which lasted at least 24 h after an experimental disturbance) were categorized as follows: (1) adopted by another pair; (2) pecked to death (observed or carcass with head laceration); (3) died on territory with no signs of pecking; and (4) unaccountably disappeared from the plot. Before each disturbance, I recorded the number of chicks at each nest in each plot. During and after the disturbance, I noted each death. Afterward, I identified the parentage of a dead chick, if unknown, using four indicators: (1) the location of the killing; (2) the estimated age of the chick and the number of chicks in similar-aged broods; (3) occasionally, the direction the chick was heading before death (chicks returning sue-
cessfully showed persistent directional running toward the natal territory); and (4) changes in the number of chicks attended by each pair of gulls. I also followed the fates of broods for 210 h during other behavioral observations lasting at least 4 h each day until early July when my watches became shorter.

Reproductive performance, 1977.—To establish the effects of human disturbance on reproduction, I recorded several measures of reproductive performance in each plot. Hatching success (number of eggs hatched/number of eggs laid) in the moderately and most disturbed plots was determined from the data collected during disturbances. I documented fledging success (number of chicks fledged/number of eggs hatched) for the moderately and most disturbed plots from the blind. Hatching and fledging success in the least disturbed plot were determined from the blind by noting the number of eggs and/or chicks for each pair. With two exceptions (two chicks of 26 days of age from a late nest), a chick was considered fledged at the age of 35 days when many Ring-billed Gulls are capable of flight. I counted all chicks which were hatched in the plot (color-marked with dye) and fledged from the plot as fledglings even though some individuals were adopted and reared by foster parents in the plot. I excluded from the analysis all undyed chicks from outside the plots that were adopted by pairs in the plot. I also excluded all chicks that hatched in the plot but were reared outside the plot by foster parents because I could not monitor their fates after adoption. Two chicks in the least disturbed plot were pecked to death by their parents after adoption of foreign chicks which were displaced from the adjacent, most disturbed plot during my assistant’s visits. I therefore eliminated these deaths from the analysis of reproductive performance. I excluded the data from two late nests (probably renests) in the least disturbed plot because I could not determine the number of eggs or young in the nests which were partially obscured by vegetation. I use net reproductive output (number of chicks fledged/number of eggs laid) as a measure of overall reproductive performance.

To compare reproductive performance and behavior between plots, I divided the data into quarters based on the hatching date for the first egg hatched in each nest. I refer to first quarter gulls as ‘early,’ second and third quarter nesters as ‘mid-season,’ and fourth quarter birds as ‘late.’

Reproductive Performance in Other Years

To determine whether reproductive performance depended more on the level of human disturbance during the post-hatching period, on the year data were gathered or on the colony in which it was obtained, I report reproductive performance from Mugg’s Island in 1976 and 1978 as well as from the Eastern Headland in 1980.

Mugg’s Island, 1976, 1978.—In 1976, nest checks continued every second day until eggs in all nests hatched or until 35 days after the nest had been initiated. Chicks were not
weighed, banded or marked with dye. In contrast with 1976, nest checks in 1978 were discontinued after the first egg pipped and study plots were not approached during entry to and departure from the blind. Hatching success was determined during visits in 1976 and from the blind in 1978. I counted the number of fledglings at each nest from the blind in both years.

*Eastern Headland, 1980.*—On Mugg’s Island I observed that gull families remain in close spatial proximity until chicks are at least 40 days of age. I considered a family to be one or more chicks accompanied by at least one adult within one body length of the young. When the oldest gull chicks were about 42 days of age on the Eastern Headland, I counted family sizes from a 2-m step ladder concealed among 8–12 m cottonwoods (*Populus deltoides*) about 10 m from the sampling area. Most gulls were sitting in groups of one to three young with one or two adults. I did not count groups of chicks unattended by an adult because chicks from different broods sometimes huddle together when their parents are absent.

This sampling method does not account for nests that failed completely, i.e., produced no fledglings, so the estimate of fledglings per nest must be scaled downward. Excluding the most disturbed plot in 1977, the average rate of nest failure in six plots during 1976–1978 on Mugg’s Island was 7.8% (SD = 6.6). Assuming that there was a similar rate of nest failure on the Headland in 1980, it is likely that 13 nests failed completely. Thirteen nests with zero offspring were therefore added to the 172 families with at least one chick before I calculated the number of fledglings per nest.

**RESULTS**

**Observation of Investigator Activity, 1977**

*Nesting chronologies.*—Different nesting chronologies in the least, moderately, and most disturbed plots could affect interplot comparisons of behavior and reproductive performance. Interplot comparisons of laying and hatching chronologies revealed no significant differences (Kolgomorov–Smirnov tests, *P* > 0.05). Egg-laying began on 19 April in all plots and ended on 23 May in the moderately disturbed plot, on 30 May in the most disturbed plot, and on 29 May in the least disturbed plot (excluding two renests). The peak of egg-laying in all plots occurred between 26 and 30 April. The hatching period began on 15 May in all three plots and ceased on 15 June in the moderately disturbed plot, on 5 June in the most disturbed plot, and on 20 June in the least disturbed plot. The peak of hatching in all plots occurred between 20 and 24 May. Observations of the laying and hatching periods in other parts of the colony suggested that the study plots were synchronous with the entire colony.

*Behavioral responses of the gulls—interplot comparisons.*—To standardize the data, the number of fights was divided by the number of gull pairs represented by at least one adult on the territory during each experimental disturbance and by minutes of observation, i.e., 30 min for pre- and post-disturbance observation periods or by the duration of the disturbance observation period. The number of attacks on chicks and chick runs were each divided by the number of chicks in the plot during each experimental
disturbance and by minutes of observation or by the duration of the disturbance.

Adult fights, chick runs, and attacks on chicks occurred rarely before disturbance, very frequently during disturbance, and commonly after disturbance in the moderately and most disturbed plots but only rarely in the least disturbed plot (Table 2). Gulls in all plots behaved similarly before disturbance began, exhibiting few of the monitored behaviors (Table 2: ANOVAs, \( P > 0.05 \)). Behavior was similar in the moderately and most disturbed plots for the disturbance or post-disturbance observation periods (ANOVA, \( P > 0.05 \)). In contrast, almost all behaviors were significantly more frequent in these plots compared to the pre-disturbance and post-disturbance observation periods in the least disturbed plot (\( t \)-tests, \( P < 0.05 \)). Pecking rate after disturbance in the moderately disturbed plot was not higher than in the least disturbed plot (\( P < 0.10 \)).

Behavioral responses of the gulls—intraplot comparisons.—There were no significant differences in behavior between the pre- and post-disturbance observation periods in the least disturbed plot (Table 2). In the moderately disturbed plot, adult fighting, chick runs, and attacks on chicks were more frequent during disturbance than in the pre- and post-disturbance observation periods (\( t \)-tests, \( P < 0.01 \)). Pecks per attack and chick running were more frequent after disturbance than before (\( t \)-tests, \( P < 0.05 \)), whereas adult fights and adult attacks on chicks (\( P < 0.10 \)) did not differ for pre- and post-disturbance observation periods in the moderately disturbed plot.

In the most disturbed plot, chick runs, attacks on chicks, and pecking rate were higher during and after disturbance than before human intrusion (\( t \)-tests, \( P < 0.01 \); Table 2). Adult fights were more frequent during disturbance than in the pre-disturbance observation period (\( t = 5.06, \text{df} = 8, P < 0.01 \)), but not different between the pre- and post-disturbance observation periods. All behavior measures except pecking rate were greater during disturbance than after in the most disturbed plot (\( t \)-tests, \( P < 0.01 \)). Pecking rate remained at comparable levels during and after investigator entry.

Behavioral responses of the gulls—temporal patterns.—Adults became more aggressive and chicks ran more often in the more frequently disturbed plots over the course of investigator visits whereas the behavior of least disturbed gulls remained relatively constant. There were no significant trends in any plot for pre-disturbance observation periods. In the moderately disturbed plot, fights, attacks on chicks, and chick runs became more frequent later in the experiment during disturbances (Spearman rank correlations, \( P < 0.05 \)) whereas only adult fights increased
<table>
<thead>
<tr>
<th>Plot</th>
<th>Adult fights$^a$</th>
<th>Chick runs$^a$</th>
<th>Attacks on chicks$^a$</th>
<th>Pecks/attack</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>pre-</td>
<td>during</td>
<td>post-</td>
<td>pre-</td>
</tr>
<tr>
<td>Least</td>
<td>0.02$^b$</td>
<td>—</td>
<td>0.03</td>
<td>0.00</td>
</tr>
<tr>
<td>disturbed</td>
<td>±0.02</td>
<td>±0.04</td>
<td>±0.04</td>
<td>±0.00</td>
</tr>
<tr>
<td>Moderately</td>
<td>0.03$^c$</td>
<td>3.49$^{c,d,e}$</td>
<td>0.35$^c$</td>
<td>0.00</td>
</tr>
<tr>
<td>disturbed</td>
<td>±0.04</td>
<td>±2.60</td>
<td>±0.29</td>
<td>±0.00</td>
</tr>
<tr>
<td>Most</td>
<td>0.04</td>
<td>5.61$^{c,d,e}$</td>
<td>0.96$^c$</td>
<td>0.00</td>
</tr>
<tr>
<td>disturbed</td>
<td>±0.06</td>
<td>±3.01</td>
<td>±1.06</td>
<td>±0.00</td>
</tr>
</tbody>
</table>

$^a$ Values shown were multiplied by 100.

$^b$ All values are mean ± 1 SD.

$^c$ Statistically different (t-tests, $P < 0.05$) from the same behavior before and after disturbance in the least disturbed plot.

$^d$ Statistically different (t-tests, $P < 0.05$) from the same behavior before disturbance in the same plot.

$^e$ Statistically different (t-tests, $P < 0.05$) from the same behavior after disturbance in the same plot.
throughout the experiment during the post-disturbance observation period ($r_s = 0.66$, df = 9, $P < 0.05$). In the most disturbed plot, adult fights, attacks on chicks, pecks per attack, and chick runs increased throughout the experiment during and after disturbances (Spearman rank correlations, $P < 0.05$).

**Chick fates, 1977.**—The number of chicks dying on territory was similar in all plots (Table 3). However, adoptions ($\chi^2 = 41.67$, df = 1, $P < 0.005$), chick disappearances ($\chi^2 = 18.61$, df = 1, $P < 0.005$), and pecking deaths ($\chi^2 = 33.38$, df = 1, $P < 0.005$) were more common in the most disturbed plot than in the least disturbed area. Similarly, these chick fates occurred more in the moderately disturbed plot than in the least disturbed plot (adoptions: $\chi^2 = 12.19$, df = 1, $P < 0.005$; disappearances: $\chi^2 = 6.98$, df = 1, $P < 0.01$; pecking deaths: $\chi^2 = 9.18$, df = 1, $P < 0.005$). Chicks in the most disturbed plot were adopted ($\chi^2 = 10.04$, df = 1, $P < 0.005$) and pecked to death ($\chi^2 = 8.06$, df = 1, $P < 0.005$) more frequently than those in the moderately disturbed plot.

To determine whether each chick fate occurred at different times during the experiment, I compared the dates on which adoptions, chick killings, chick deaths on territory, and disappearances occurred for each plot. There were no differences in date of occurrence for any of these chick fates in the least disturbed plot (Table 3). In the moderately disturbed plot, adoption and disappearance occurred nearest the onset of hatching, death on the territory ranked third, and chick killings occurred latest. Adoption ($t = 3.96$, df = 32, $P < 0.01$), disappearance ($t = 4.36$, df = 29, $P < 0.01$),

### Table 3

**Fates of Chicks and Mean Date of Occurrence for Each Fate in Each Study Plot in 1977**

<table>
<thead>
<tr>
<th>Plot</th>
<th>Adopted inside plot</th>
<th>Adopted outside plot</th>
<th>Died on natal territory</th>
<th>Pecked to death</th>
</tr>
</thead>
<tbody>
<tr>
<td>Least disturbed</td>
<td>2 (0)$^a$</td>
<td>0 (0)$^a$</td>
<td>2 (0)$^a$</td>
<td>2 (0)$^{a,b}$</td>
</tr>
<tr>
<td>(21 May)</td>
<td>(25 May)</td>
<td>(30 May)</td>
<td>(8 June)</td>
<td></td>
</tr>
<tr>
<td>Moderately disturbed</td>
<td>7 (1)$^a$</td>
<td>10 (0)$^a$</td>
<td>12 (3)$^a$</td>
<td>16 (0)$^a$</td>
</tr>
<tr>
<td>(25 May)$^d$</td>
<td>(25 May)$^d$</td>
<td>(26 May)$^c$</td>
<td>(30 May)$^{c,d}$</td>
<td></td>
</tr>
<tr>
<td>Most disturbed</td>
<td>6 (0)$^a$</td>
<td>22 (0)$^a$</td>
<td>15 (0)$^a$</td>
<td>25 (0)$^a$</td>
</tr>
<tr>
<td>(23 May)$^d$</td>
<td>(21 May)$^d,e$</td>
<td>(26 May)$^d$</td>
<td>(29 May)$^{d,e}$</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ The number in parentheses represents chick losses after experimental disturbances were stopped.

$^b$ These deaths were caused by adoption of chicks from the most disturbed plot (see text).

$^c$ $t$-test, $P < 0.05$.

$^d$ $t$-test, $P < 0.01$.

$^e$ $t$-test, $P < 0.001$. 
### Table 4
Reproductive Performance for Each Quarter of Post-hatching Period in Each Plot on Mugg’s Island in 1977

<table>
<thead>
<tr>
<th>Plot</th>
<th>Quarter of the season</th>
<th>Eggs laid</th>
<th>Eggs-hatched (hatching success) %</th>
<th>Fledglings (fledging success) %</th>
<th>Net reproductive output %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Least disturbed</td>
<td>1</td>
<td>61</td>
<td>59 (97)</td>
<td>58 (98)</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>63</td>
<td>62 (98)</td>
<td>62 (100)</td>
<td>98</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>61</td>
<td>53 (87)</td>
<td>49 (93)</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>60</td>
<td>53 (88)</td>
<td>46 (90)^a</td>
<td>79^a</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>245</td>
<td>227 (93)</td>
<td>215 (95)^a</td>
<td>89^a</td>
</tr>
<tr>
<td>Moderately disturbed</td>
<td>1</td>
<td>54</td>
<td>49 (91)</td>
<td>40 (82)</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>56</td>
<td>52 (93)</td>
<td>43 (83)</td>
<td>77</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>57</td>
<td>50 (88)</td>
<td>39 (78)</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>57</td>
<td>50 (88)</td>
<td>33 (66)</td>
<td>58</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>224</td>
<td>201 (90)</td>
<td>154 (77)</td>
<td>69</td>
</tr>
<tr>
<td>Most disturbed</td>
<td>1</td>
<td>40</td>
<td>34 (85)</td>
<td>16 (47)</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>39</td>
<td>37 (95)</td>
<td>28 (76)</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>39</td>
<td>30 (77)</td>
<td>16 (53)</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>39</td>
<td>23 (59)</td>
<td>11 (48)</td>
<td>28</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>157</td>
<td>124 (79)</td>
<td>71 (57)</td>
<td>45</td>
</tr>
</tbody>
</table>

^a Percentages calculated after excluding two chicks pecked to death by their own parents (see text).

and death on the territory ($t = 2.32, df = 20, P < 0.05$) were significantly earlier events than chick killings.

The pattern was very similar in the most disturbed plot, where adoptions occurred earlier than pecking deaths ($t = 2.88, df = 51, P < 0.01$) and disappearances were earlier than pecking deaths ($t = 8.73, df = 38, P < 0.001$) and deaths on territory ($t = 3.00, df = 20, P < 0.01$). Thus, chick fates tended to occur in the following temporal sequence: disappearance, adoption, deaths on territory, and chick killing.

**Reproductive Performance, 1977**

Hatching success in the most disturbed plot was lower than in the least and moderately disturbed plots ($\chi^2 = 16.32, df = 2, P < 0.005$; Table 4). Birds in the most disturbed plot had the lowest fledging success, those in the least disturbed plot had the highest, and those in the moderately disturbed area had intermediate success ($\chi^2 = 71.32, df = 2, P < 0.005$; Table 4). Net reproductive output followed the same pattern ($\chi^2 = 83.43, df = 2, P < 0.005$).

Late nesters in the least disturbed plot had poorer reproductive perfor-
TABLE 5

Reproductive Performance of Ring-billed Gulls in Investigations During which Study Plots were Entered Frequently Throughout Nesting Season

<table>
<thead>
<tr>
<th>Study site or lake</th>
<th>Year</th>
<th>Total nests</th>
<th>Hatching success Mean (%)</th>
<th>Fledging success Mean (%)</th>
<th>Fledglings per nest Mean</th>
<th>Fledglings per egg laid Mean (%)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mackinac Str.,</td>
<td>1952</td>
<td>16</td>
<td>—</td>
<td>31</td>
<td>67</td>
<td>22</td>
<td>Emlen (1956)</td>
</tr>
<tr>
<td>Miquelon L.,</td>
<td>1964</td>
<td>87</td>
<td>86</td>
<td>34</td>
<td>1.00</td>
<td>29</td>
<td>Emlen (1956)</td>
</tr>
<tr>
<td>Alberta</td>
<td>1965a</td>
<td>436</td>
<td>16</td>
<td>00</td>
<td>00</td>
<td>00</td>
<td>Emlen (1956)</td>
</tr>
<tr>
<td>L. Huron</td>
<td>1972</td>
<td>80</td>
<td>63</td>
<td>87</td>
<td>1.54</td>
<td>55</td>
<td>Duxheimer and Southern</td>
</tr>
<tr>
<td>L. Huron</td>
<td>1972</td>
<td>107</td>
<td>60</td>
<td>70</td>
<td>1.19</td>
<td>42</td>
<td>Duxheimer and Southern</td>
</tr>
<tr>
<td>L. Ontario</td>
<td>1977</td>
<td>155</td>
<td>78</td>
<td>81</td>
<td>1.84</td>
<td>63</td>
<td>Chardine (1978)</td>
</tr>
<tr>
<td>Granite Is.,</td>
<td>1976</td>
<td>144</td>
<td>89</td>
<td>58</td>
<td>1.53</td>
<td>52</td>
<td>Somppi (1978)</td>
</tr>
<tr>
<td>L. Superior</td>
<td>1977</td>
<td>405</td>
<td>62</td>
<td>67</td>
<td>1.04</td>
<td>33</td>
<td>Somppi (1978)</td>
</tr>
<tr>
<td>E. Headland,</td>
<td>1977</td>
<td>183</td>
<td>81</td>
<td>40b</td>
<td>1.35b</td>
<td>33b</td>
<td>Haymes and Blokpoel (1978)</td>
</tr>
<tr>
<td>L. Ontario</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mugg’s Is.,</td>
<td>1976</td>
<td>166</td>
<td>82</td>
<td>79</td>
<td>1.76</td>
<td>65</td>
<td>this study</td>
</tr>
<tr>
<td>L. Ontario</td>
<td>1977c</td>
<td>75</td>
<td>90</td>
<td>77</td>
<td>2.05</td>
<td>69</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1977d</td>
<td>53</td>
<td>79</td>
<td>58</td>
<td>1.34</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min-max</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60-90</td>
<td>31-87</td>
<td>0.67-2.05</td>
</tr>
<tr>
<td>SD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11</td>
<td>20</td>
<td>0.41</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>11</td>
<td>11</td>
</tr>
</tbody>
</table>

* Data excluded from total and mean.

b N = 93.

c Moderately disturbed plot.

d Most disturbed plot.

mance than early or mid-season nesters (hatching success: $\chi^2 = 9.18$, df = 3, $P < 0.005$; fledging success: $\chi^2 = 8.31$, df = 3, $P < 0.01$; net reproductive output: $\chi^2 = 17.42$, df = 3, $P < 0.005$; Table 4). There were no seasonal differences for reproductive performance in the moderately disturbed plot even though late nesters tended to have lower success. In the most disturbed plot, hatching success was lower for late nesters ($\chi^2 = 16.30$, df = 3, $P < 0.005$) whereas net reproductive output was lower for early and late breeders ($\chi^2 = 16.36$, df = 3, $P < 0.005$). Fledging success followed a pattern similar to net reproductive output ($P < 0.10$).

Reproductive Performance in Other Years

Hereafter, I use the term ‘traditional disturbance’ when referring to studies in which investigators (including myself) entered study areas at
least every second day throughout the breeding season. I distinguish these studies from some of the research reported here by using the term ‘minimal disturbance’ to refer to circumstances where I reduced or eliminated investigator disturbance during the post-hatching period.

Mugg's Island 1976–1978 and Eastern Headland 1980.—Using minimal disturbance techniques on Mugg’s Island (1977—least disturbed plot, 1978—plot three) and on the Eastern Headland, reproductive performance was consistently better than when I followed traditional methods (Mugg’s Island, 1976—plots one, two, and three; 1977—moderately and most disturbed plots; Tables 5 and 6). After minimizing disturbance, hatching success averaged 8% higher, fledging success averaged 19% higher, fledglings per nest averaged 36% higher, and net reproductive output averaged 26% higher.

When the gulls were not disturbed during post-hatching on Mugg’s Island in 1978, late nesters had lower fledging success than early or mid-season nesters ($\chi^2 = 10.59$, df = 3, $P < 0.05$), but hatching success and net reproductive output did not vary significantly with time of hatching ($P < 0.10$; Table 7).

Reproductive Performance in Other Studies

Reproductive performance for Ring-billed Gulls investigated under traditional disturbance conditions in this and other studies varied considerably (Table 5) but was consistently higher under minimal disturbance conditions than under traditional disturbance conditions (fledging success 52% higher, Mann-Whitney $U$-test, $P < 0.05$; fledglings per nest 71% higher,
Table 7
Reproductive Performance for Each Quarter of Post-hatching Period in 1978

<table>
<thead>
<tr>
<th>Quarter of the season</th>
<th>Eggs laid</th>
<th>Eggs hatched (hatching success)</th>
<th>Fledglings (fledging success)</th>
<th>Net reproductive output</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>28</td>
<td>25 (89)</td>
<td>23 (92)</td>
<td>82</td>
</tr>
<tr>
<td>2</td>
<td>29</td>
<td>26 (90)</td>
<td>25 (96)</td>
<td>86</td>
</tr>
<tr>
<td>3</td>
<td>32</td>
<td>24 (75)</td>
<td>24 (100)</td>
<td>75</td>
</tr>
<tr>
<td>4</td>
<td>31</td>
<td>24 (77)</td>
<td>18 (75)</td>
<td>58</td>
</tr>
</tbody>
</table>

Mann-Whitney U-test, \( P < 0.05 \); and net reproductive output 76% higher, Mann-Whitney U-test, \( P < 0.05 \); Tables 5, 6). Only hatching success was not significantly higher when disturbance was minimized.

Discussion

Observation of Investigator Activity and Gull Behavior, 1977

Confounding factors.—Interplot differences in nesting chronology, age composition, gull density or vegetation may have affected the results. Nesting chronologies for each plot were similar, so any behavioral differences due to different temporal patterns of egg-laying and/or hatching should have been consistent across plots. Judging by the proportion of pairs with one member having immature plumage (black pigment in rectrices, brown primaries without white spots, brown feathers on breast, belly, or head), each plot had a similar age composition (least disturbed plot [17%], moderately disturbed plot [12%], most disturbed plot [13%]). Nesting density was highest in the least disturbed plot (0.7 nests/m²), intermediate in the moderately disturbed plot (0.6 nests/m²) and lowest in the most disturbed plot (0.5 nests/m²). The high fledging success in the least disturbed plot demonstrates that density-dependent chick mortality was not an important factor when human activity was curtailed.

Sparse willows grew near the edges of the least and moderately disturbed plots and were absent in the most disturbed area, but the vegetation provided very little cover. When chicks ran from their natal territories, they infrequently used willows for cover so confounding effects were probably minimal. Proportionately more pairs in the most disturbed (75%) and moderately disturbed (65%) plots nested in the driftwood half of the plot than in the least disturbed plot (52%). Driftwood provided more hiding places for chicks during disturbance than open areas so relatively more young in the more disturbed plots could have benefitted from driftwood.
Generally then, confounding factors were of minor importance compared to the effects of investigator activity.

Behavioral responses of the gulls.—Human activity grossly altered adult and chick behavior. Adults fought 10–15 times more often during disturbance than before and attacks on chicks increased between 400 and 600 fold. I never observed a chick run during pre-disturbance watches and yet runs were very common during and after disturbance. Chick running and adult attacks persisted at high levels after investigator activity. As a result, most pecking deaths occurred after disturbance because adult fighting subsided compared to disturbance observations and running chicks became easier targets for attack.

Chick running during investigator visits has been reported in many Laridae (Herring Gull: Paynter 1949, Tinbergen 1960; Glaucous-winged Gull: Vermeer 1963, Gillett et al. 1975; Western Gull: Robert and Ralph 1975; Ring-billed Gull: Emlen 1956; California Gull [L. californicus]: Vermeer 1970; Heermann’s Gull [L. heermanni]: Anderson and Keith 1980; Sooty Tern [Sterna fuscata]: Ashmole 1963). I have observed chick running in response to my presence in Herring Gull, Caspian Tern (S. caspia), and Common Tern (S. hirundo) colonies. Thus, chick running resulting from human activity may be the rule among terrestrial-nesting larids.

In this study, chick running caused by investigator activity combined with seasonal differences in adult behavior and resulted in different chick fates. Early in the post-hatching period running chicks were either adopted by incubating or brooding adults or they ran long distances (usually >5 m) from their territories and disappeared. Chicks that were not adopted probably starved to death or died of exposure elsewhere in the colony. Later in the post-hatching period, chicks ran more often and increasingly hostile neighbors frequently killed chicks of fewer than 10 days of age. These seasonal differences in chick mortality contributed to different reproductive performance for early, mid-season, and late nesters in the most disturbed plot. Adult aggression increases in other terrestrial nesting larids as chicks become more mobile (Western Gull: Hunt and Hunt 1975; Herring Gull: Burger 1980, Fetterolf, unpubl.; Ring-billed Gull: Fetterolf 1981). As in this study, disturbance in previous investigations may have amplified adult aggression leading to artificially higher rates of pecking death for late hatching chicks.

In contrast to disturbed situations, increases in adult aggressiveness during the post-hatching period (Fetterolf 1981) resulted in very few chick deaths from neighbor attack in undisturbed conditions (Fetterolf, in press). During 1976–1978, I observed undisturbed Ring-billed Gulls for more than 450 h and saw only three pecking deaths while watching more than 1100 chicks being reared (Fetterolf, in press). I saw no pecking deaths in more
than 200 h of observation on 55 pairs of minimally disturbed Herring Gulls in 2 years. In both these species, brood reductions of other kinds were also uncommon when human activity was rare or eliminated after hatching began. Young in artificially smaller broods resulting from investigator disturbance probably had less intra-brood competition for provisions than chicks in minimally disturbed broods and thus attained better physical condition (e.g., greater fat stores) at fledging.

Other potentially important biases resulted from a high frequency of adoption which is rare under minimal disturbance conditions. On two occasions, adoptive parents with eggs pecked their newly hatched chicks to death. Parents with young chicks often adopted chicks larger (older) than their own. Victims of this artificially skewed competition usually appeared thin and weak and occasionally seemed to starve to death. Measures of chick quality such as growth rate, weight at fledging, fat load, etc., could be seriously biased by unnatural brood reductions and adoptions, thus creating severe interpretational problems (in parental investment research for example, Trivers 1972).

Reproductive Performance, 1977

Hatching success was lowest in the most disturbed plot where nest checks were shortest before the post-hatching period. Longer disturbances and direct entry to the plot during experimental disturbances in post-hatching therefore reduced hatching success compared to the moderately and least disturbed plots. Entering the plot increased adult fighting which forced incubators off nests more frequently for longer periods and probably increased embryonic mortality due to excessive cooling or heating.

Fledging success, and consequently net reproductive output, were seriously affected by human activity. Even when investigator activity was restricted, the loss of young birds was significant. First, investigator activity in this study was limited to every second day until nearly all eggs were hatched and stopped once the youngest chicks were 7 days old. In contrast, post-hatching reproductive performance is usually assessed by entering study areas at least every second day until all chicks reach a minimum of 21–37 days of age (Vermeer 1970, Dexheimer and Southern 1974, Chardine 1978, Haymes and Blokpoel 1978, this study 1976). Second, human activity was also restricted in the moderately disturbed plot by limiting the duration of visits and by walking the perimeter of the plot. Nevertheless, chick losses were high.

Reproductive Performance in Other Years and Other Studies

Hatching success on Mugg’s Island in 1976 and 1978 was comparable and intermediate between the most disturbed plot and moderately dis-
turbed plots in 1977. Interyear differences in age composition (pairs in adult plumage, 1976—39%, 1978—100%) and nocturnal predation (nightly visits by a Great Horned Owl [Bubo virginianus] in 1978) confound interpretations regarding the impact of human disturbance. No doubt such differences exist among investigations as well, so low hatching success often reported in other studies could be attributable to more frequent or prolonged human disturbance or to other factors.

Generally, fledging success, fledglings/nest, and net reproductive output on Mugg's Island in 1976 and 1977 (moderately and most disturbed plots) fell within the range of values reported in past research but were demonstrably lower than in less disturbed situations. In a similar 2-year study of human disturbance in Herring Gulls, I found fledging success of 81–100%, and net reproductive output of 81–91% in plots that were rarely entered during the post-hatching period (Fetterolf 1979b). By comparison, in plots that were disturbed regularly throughout post-hatching, fledging success was 46–50% and net reproductive output was 24–37%. Caspian Terns also have remarkably high fledging success (90–98%) and net reproductive output (78–79%) when they are not disturbed by investigators during the post-hatching period (Fetterolf and Blokpoel, in press). Infrequently disturbed Glaucous-winged Gulls had about 89% fledging success compared to 73% for birds that were more frequently disturbed (Gillett et al. 1975). Young of the cliff-nesting Black-legged Kittiwake (Rissa tridactyla) do not run (Cullen 1957) and fledging success of kittiwakes approaches 90% even for pairs nesting for the first time (Wooler and Coulson 1977).

The high fledging success in minimally disturbed studies is exceptional compared to traditional studies of terrestrial-nesting Laridae (e.g., Paynter 1949, Vermeer 1963, Harris 1964, Kadlec and Drury 1968, Kadlec et al. 1969, Hunt and Hunt 1976; see Table 5). Reduced reproductive performance resulting from human activity has been reported by Hunt (1972), Robert and Ralph (1975), Gillett et al. (1975), Hand (1980), and Anderson and Keith (1980). Although frequent disturbances by a mammalian predator such as a fox (Vulpes sp.) might induce similar mortality in larids, the combination of human disturbance, increasing adult aggression, and increasing chick mobility may have caused artificial chick losses in previous studies which cannot be separated from real biological effects.

Seasonal patterns as well as the amount of chick mortality may be affected by human disturbance. When nesters were rarely disturbed in 1977 or not disturbed in 1978 during post-hatching, late nesters had lower reproductive performance. A similar seasonal pattern of reproductive performance has been found in other investigations on gulls (see Parsons 1975, Morris and Haymes 1977 for reviews). Evidence presented here sug-
gests that this pattern in previous studies may have been enhanced but not modified by human disturbance. Also in support of this interpretation, Robert and Ralph’s (1975) results show that late hatching eggs in frequently disturbed plots had lower hatching success and higher losses of young chicks than late hatching eggs in less frequently disturbed areas. Patterson (1965) reported that early and late Black-headed Gulls (L. ridibundus) had lower reproductive performance and Parsons (1971) attributed higher early and late season chick mortality in Herring Gulls to cannibalism. High mortality for early and late nesters occurred in the most disturbed plot in 1977 but was not apparent under minimal disturbance conditions, so this pattern may have been created by human disturbance in some previous investigations.

Theoretical considerations.—Since the development of sound theory regarding the evolution of reproductive strategies in colonial birds depends upon real unbiased biological patterns of mortality, human activity has potentially caused numerous biases. Has investigator activity changed the probability of survival to reproductive age of individual chicks (effective survivorship)? The question is important because if effective survivorship is not changed by human disturbance, human activities would have no negative impact on population dynamics or on biological theory. My data provide no direct answer to the question but suggest that effective survivorship is changed by human disturbance. For example, chick death could have been random instead of the result of selection acting against inferior (in the absence of disturbance) individuals. Second, chick death could have been non-random resulting from selection against individuals that behaved in a more ‘life-threatening’ manner during human disturbance. Finally, artificial brood reductions may enhance effective survivorship of individuals remaining with their parents whereas increases in brood-size due to adoption may have the opposite effect. I believe these findings, in concert with those of previous investigators (e.g., Gillett et al. 1975, Robert and Ralph 1975) compel future researchers of terrestrial-nesting larids to ask: how successful are the birds when they are undisturbed by humans during the post-hatching period (see Duffy 1979)?

SUMMARY

I documented the effects of human disturbance on gull (Larus sp.) behavior and reproductive performance in two different colonies between 1976 and 1980 by observing gull behavior and reproductive performance during periods with different levels of investigator activity. Human disturbance precipitated changes in gull behavior which caused significant reductions in fledging success, fledglings per nest, and net reproductive output even when disturbance was limited. In contrast, areas which were relatively undisturbed during the post-hatching period in 3 years and two colonies had very few chick deaths. Human disturbance caused adoptions and enhanced seasonal patterns of chick mortality. I conclude that
human-induced chick losses could have had confounding effects in most past studies involving larid reproductive success and may seriously confound theoretical interpretations of reproductive strategies in terrestrial-nesting colonial birds.

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LITERATURE CITED


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DISPLAYS AND VOCALIZATIONS OF THE SORA AND THE VIRGINIA RAIL

GERALD W. KAUFMANN

Little is known about the ecology and the behavior of the Rallidae. Being shy birds which live in dense vegetation and rarely fly unless forced to do so, most species of rails are more often heard than seen. Most of the information available pertains to coots (Fulica spp.) and the gallinules (Gallinula spp., Prophyrus spp., Porphyrio spp.), species that regularly feed and move about in open areas (Howard 1940; Gullion 1952, 1953, 1954; Kornowski 1957; Askaner 1958; Navas 1960; Holyoak 1970; Wood 1974). The present study concerns the social behavior of the Sora (Porzana carolina) and the Virginia Rail (Rallus limicola), especially their methods of communicating in dense marsh vegetation.

METHODS


Most observations were made from blinds placed near nests. Twelve nests were observed during 149 h. Rails trapped in the vicinity of a blind were marked with paint or plastic nasal tabs so as to be individually identifiable. Sex was determined by size, males being slightly larger in both species (Horak 1964).

Captive rails were studied during the 1967–1969 breeding seasons in an outdoor flight pen on the Cedar Creek Natural History Area (Kaufmann 1977). Observation of these birds provided most of the information on social behavior, especially on the Sora. (During the three seasons five pairs of captive Soras formed pair bonds and defended territories, and three nested. One pair of Soras defended a territory each season and nested twice. Five pairs of captive Virginia Rails formed pair bonds, three defended territories, and one nested. Seventy-eight Sora copulations and 37 Virginia Rail copulations were recorded during 645 h of observation.)

Activity was filmed with a 16-mm Arriflex and a Super-8 Anscomatic camera with zoom lenses. The 16-mm films were analyzed using a Bell and Howell time-and-motion study projector. Sketches were made from movies and 35-mm photos. Vocalizations were recorded on a Magnavox tape recorder at 3.75 inches (9.5 cm)/sec. Sonograms of selected tapes were prepared on a Kay Electric Company Sona-Graph. The descriptions of the colors of the rails are from Palmer (1962).

RESULTS

Descriptions of rail behavior were based on observations of captive birds which readily defended territories and bred in a simulated marsh. The terms characterizing rail displays have been taken from studies on gulls (Laridae) (Tinbergen 1959), Moorhen (Gallinula chloropus) (Howard 1940, 1959), and Coot (Fulica atra) (Tinbergen 1959).
Fig. 1. Displays associated with hostile behavior in Soras: A. upright; B. open bill; C. forward with swanning—mild form; D. swanning—intense form; E. swanning while leaving opponent; F. swanning by raising back feathers; G. swanning by drooping wings; H. sparring; I. fighting.

Wood 1974), and American Coot (Fulica americana) (Gullion 1952). Descriptions apply to both species with the variations and exceptions noted.

Behavior associated with hostile encounters: Upright.—The bird assumes an extreme erect posture by stretching its neck upward and
straightening its legs. The opponent is faced and the bill is directed toward it. A white patch is occasionally exposed on the lesser coverts when the opponent is a dominant bird (Figs. 1A, 2A). In the Virginia Rail, the neck feathers are ruffled when the other bird responds with an “upright.” This display appears to be derived from an intention movement of pecking and frequently precedes pecking.

*Open-bill.*—This display, in which the bill is opened and pointed toward a passing bird, was seen only in the Sora (Fig. 1B). It was most commonly seen during the nonbreeding season when two birds were close to one another and individual distance was seemingly violated.

*Facing away.*—The head is lowered and turned to one side, the bill pointing toward the substrate. “Facing away” was given as a response to a mild threat, such as the “forward” (see below) and frequently appeared to inhibit attack. It was also performed when a bird was being preened by its mate (Figs. 3B, 4B).

*Forward.*—The head is stretched forward, toward the opponent (Figs. 1C, 2B). Virginia Rails seem to extend the neck farther than Soras. Soras
usually included a variety of feather erection postures in a forward when two males were engaged in display at the boundaries of their territories. A forward appears to be derived from an incipient “chase” (see below), and a chase usually follows if the opponent does not flee.

Swanning.—This was a highly variable and dynamic display given when
Soras of the same sex, usually males, met at territorial boundaries. Here the birds alternately faced and turned away from each other. When one bird approached the boundary, the other usually faced him in a forward; if one bird began to leave, the other also turned away. "Swanning" was interspersed with uprights, "substrate pecking" and fighting.

During intense swanning the contour feathers are fluffed, the scapulars and back feathers are raised above the back by lifting up the wings, and the undertail coverts are spread upward and laterally (Fig. 1D). Frequently the body was either tilted away from the opponent or the feathers were sleeked on the side facing the opponent and ruffled on the opposite side. Maximum spreading of the undertail coverts occurred when one bird turned away from its opponent, especially at the end of a territorial
dispute (Fig. 1E). On several occasions the back feathers were raised while the wings were held close to the body (Fig. 1F).

At times the primaries were exposed during swanning when the wings were drooped as both the tail and posterior part of the body were raised (Fig. 1H). This form of swanning occurred when I placed a dead Sora, frozen in an upright position, in another Sora’s territory and when I disturbed a bird at its nest. A similar form of primary exposure occurred on several occasions during slow retreats of territory-holding birds after intrusion in another’s territory. The wings were lifted from the back and the primaries were extended posteriorly above the tail (Fig. 1E). The retreating bird moved slowly, straightening its legs so that it appeared to be walking on stilts.

The black facial mask of the Sora, as probably viewed by an opponent provides a striking contrast with the yellow bill, which occasionally has an added touch of orange to scarlet-orange near the nares. Perhaps the face mask reinforces threat displays in which opponents face each other, since the facial coloration is heightened during the breeding season. During the nonbreeding season the reddish-brown irides turn brown and become more distinguishable from the mask and the bill shrinks slightly as it changes to a duller greenish-yellow.

At the end of an encounter, as the two birds simultaneously began to leave the territorial boundary, the feathers were slowly lowered to the normal position. The retreating birds were usually substrate pecking, and as they walked away the form of pecking more closely resembled that of normal feeding. Eventually real feeding movements occurred.

Although Virginia Rails fanned and dropped their wings during several hostile encounters, they did not demonstrate a boundary display comparable to that of Soras. It is possible that Virginia Rails would have exhibited as prolonged and elaborate swanning displays as the Soras, had two pairs of the former species bred synchronously. Virginia Rails perform swanning of short duration during chasing, pecking, and fighting. Swanning of longer duration occurs when chases end abruptly and when there is thwarting of an attack. Longer swanning occurred in three situations: (1) when a bird stopped chasing at its territorial boundary; (2) when a female ran to chase a male which was attacking her mate; and (3) when a rail ran toward me as I approached its nest (Fig. 2C). During longer swanning the wings are held laterally with the primaries and secondaries fanned and pointing upward and the chestnut upper wing coverts turned forward.

I suggest that swanning be used as a general descriptive term for all hostile behavior of Rallidae in which the wings are raised above the back,
appear to be raised by ruffling of rump feathers, or are spread laterally or downward. Observations of rails during boundary disputes and of investigators approaching nests indicated that swanning is a complex display of all possible intermediate wing postures instead of several discrete displays. Gullion (1952) first used the term “swanning” to describe the threat display American Coots directed towards other species. He described threat postures between male coots using wing arching as “paired display” because he believed it was courtship display. Wood (1974) substituted “mutual retreat” for “paired display” in his description of the Moorhen. My suggestion to standardize terminology by using swanning would include paired display of American Coots, mutual display of Moorhens, “distract display” of Virginia Rails described by Weins (1966), and “wing-lifted walk” and “wing-spread” of Yellow Rails (Coturnicops noveboracensis) described by Stalheim (1973).

Substrate pecking.—Vigorous pecking movements are made at the ground, or into mud or water, several times in rapid succession. Soras usually keep the bill closed, but Virginia Rails often have the bill open (Fig. 2D). The undertail coverts are extended laterally beyond the tail. This display is variable and intermediate movements between “substrate pecking” and either actual pecking of another bird or movements identical to feeding are observed frequently. This display appears to be derived from aggressive pecking movements superimposed upon feeding movements and likely results from redirected aggression. If a territorial male approached another male while substrate pecking, the male being approached was pecked if it did not display or flee. If two males left their territorial boundary simultaneously the form of substrate pecking gradually changed to real feeding movements.

Virginia Rails were observed substrate pecking in four situations: (1) by a bird which was threatened by a dominant; (2) after threatening another bird which refused to flee; (3) when I disturbed a bird at hatching; and (4) by both sexes after copulation. Soras usually performed substrate pecking after turning away from another Sora following a bout of swanning, or after a meeting of the members of a pair.

Chasing, wing-snapping, and churning.—“Chasing,” consisting of a rapid forward rush, was frequent in both species. Two behavior patterns were associated with chasing: (1) “wing-snapping,” which was performed by both species and (2) “churning,” which occurred only in Soras.

Wing-snapping consists of rapid flicking of the wings forward and tucking them in place. Virginia Rails performed wing-snapping during chases while Soras performed wing-snapping at the moment they stopped chasing.

Churning by Soras involved splashing water while treading rapidly with
unflexed feet. Churning was most frequently seen when a Sora approached its territorial boundary and stopped chasing. One male frequently performed churning when he was prevented from chasing another by the presence of a wire divider in the breeding pen. Males occasionally performed churning when I approached their nests. This display appears to be homologous with “churning” in the American Coot (Gullion 1952).

I am uncertain whether some Sora chases are homologous with the “spattering charge” of American Coots (Gullion 1952). During intense chases, the chasing Sora flaps its wings and splashes water with its feet, but these movements could be necessary simply to maintain balance when running over unstable substrates.

Fighting and sparring.—“Fighting” in both species consists of jumping upward as high as 30 cm and simultaneously pecking and clawing the breast of the opponent (Fig. 11, J). Soras also fight on the water or on a floating mat of vegetation in the same way as swimming coots, by clawing at each other’s breasts while lying backward supporting themselves with their wings. Fighting was most frequent between males although it occurred occasionally between females. Fights were not observed between a male and a female; either the female retreated or her mate quickly came to her aid.

Fighting occurred most frequently between two pairs of Soras which had synchronized breeding cycles and adjacent territories. Often the males met at the boundary of their territories and jumped up and down while facing each other but did not fight. This I called “sparring.” Fighting and sparring were observed infrequently in Virginia Rails, probably because only one pair nested successfully. The male of this pair often attacked his opponent’s back, raking it with his claws, striking with the edges of his wings, and repeatedly pecking the head. The subordinate male was often forced under water in the process.

Behavior associated with pairing and copulation: Mates together.—In the first stage of pair formation, the male and female stand immobile, their long body axes usually parallel, within sight of each other but seemingly ignoring each other. For the first week or so they stand 10–30 cm apart for periods of only a few min, or 0.5 to several m apart for 15–30 min. After 2–4 weeks, they begin to bathe, feed, and preen in close proximity to each other, and bodily contact is occasionally observed in the Virginia Rail (Figs. 3A, 4A).

Social preening.—“Social preening” in both species includes allopreening, autopreening, facing away, bowing, and facing the mate. Virginia Rails also perform substrate pecking and “bill nibbling” during social preening.

In the Sora, social preening was observed only between mates, but in
the Virginia Rail dominant males preened subordinate birds during the nonbreeding season. Preening bouts between members of a pair lasted 1–5 min in the Sora but were usually more prolonged in the Virginia Rail, with some bouts lasting more than 20 min.

The bird being preened usually bowed its head or turned its head to one side, similar to the “bowing and nibbling” of the American Coot (Gullion 1952) and Moorhen (Wood 1974) (Figs. 3B, 4B). The rail often remained in this position for several seconds after its mate ceased allopreening. I believe that the facial pattern of Soras functions to reinforce threat displays and so heightens hostility between mates. When members of a pair of Soras looked directly at each other during a preening bout, they rapidly bowed, faced away, or allopreened. The movements of allopreening and autopreening appeared to be executed more stiffly by the Soras, suggesting a greater degree of ritualization than in the Virginia Rail.

_bill nibbling._—This activity, in which one bird gently pecks the bill of its mate, was observed frequently in the Virginia Rail during allopreening bouts or when both birds were feeding on the same food item. “Bill nibbling” was rare in Soras during preening bouts.

_Courtship feeding._—This behavior was observed in the pair of captive Virginia Rails which bred successfully. The male gave “nasal peeps” when he found a live food item, e.g., invertebrates, and the female responded with similar calls. The male then carried the food in his bill giving nasal peeps as he approached and presented the food to the female. Several times he carried food over a distance of 9 m. The female always took the food and ate it.

_Copulation._—Before copulation the members of the pair alternately call and come together while continuing to call. The Virginia Rail gives nasal “peeps” and the Sora gives “peeps.”

Soras usually perform a preening bout prior to copulation. In the “precopulatory chase” the male walks with a slightly stiff and erect posture, and gives soft _guoo_ calls. Occasionally he moves his head forward and back, but more often his head is held rigid in a slightly higher position than normal. His undertail coverts are spread laterally so that the tail appears to have white edges.

The male Virginia Rail approaches the female in a characteristic precopulatory chase without a preliminary preening bout. He struts toward the female, with his bill pointed up and slightly opened, and gives low, guttural _growls_. His steps are executed stiffly and his legs appear to be longer than in walking or other contexts. The head and neck move backward and forward in an exaggerated manner, the throat being puffed at each backward movement of the head (Fig. 4C). The undertail coverts are spread laterally as in the Sora.
The duration of the precopulatory chases of both species seems to depend on the receptiveness of the female. During the first week after pairing, the female rejects the copulatory attempts of the male by walking, running or flying from his precopulatory approaches, often travelling several meters within their territory. She spreads her white undertail coverts during these chases. As the time of egg-laying approaches, she is more likely to stand still, dip the end of her tail into the water, and stretch her head and neck forward. The male mounts from behind and the female lowers her head, touching the substrate with the tip of her bill or dipping it into the water (Fig. 3C).

If the female does not lower her head after the male has mounted, he pecks at her crown and either she runs out from beneath him or she responds to his pecks by lowering her head. If the female is receptive she then raises her tail and lowers her head until her body forms an angle of about 45° to the horizontal. The male makes treading movements with alternate steps on her back and then copulates. During copulation, the male Virginia Rail arches his wings but the male Sora flaps his wings, apparently to maintain balance (Figs. 3D, 4D). Copulation is brief, lasting a few seconds at most and then either the male dismounts or the female runs out from under the male.

The post-copulatory movements of the male Sora include some but not all of the components of swanning: the wings are upilted, the undertail coverts are slightly ruffled and the scapulars are raised by a slight lifting of the wings. The head is lowered below the level of the body, giving the appearance of a bow (Fig. 3E). A more extreme form of bow was performed by males when mounting did not lead to copulation (Fig. 3F). After copulation, females perform a "body shake." The body shake consists of stretching the head forward, erecting the feathers, shaking the body feathers simultaneously and briefly sleeking them. The "wing shuffle" consists of raising the wings away from the body and shaking them.

The male Virginia Rail's post-copulatory movements consist of a head flick, followed by a body shake, and several substrate peckings. The female performs a wing-shuffle or a body shake, and occasionally substrate pecking.

Meeting and passing.—Prior to incubation, nearly every meeting of the member of a Sora pair begins with allopreening and ends with a copulation attempt. After egg-laying, however, meetings between the members of a pair are brief, usually at the time of changeover during incubation. The birds hurry toward one another, stop or nearly stop as they meet, and then continue on. As they come together they adopt a variety of postures. In one posture, the head and tail point downward and the back is arched, as in a bow. In the other form, the head and tail are tilted upward, giving
the bird a U shape (Fig. 3G). While both sexes were observed in both postures, the relative frequency each sex was observed in these postures was not noted because this behavior went unnoticed until near the end of the study. These postures appear to correspond to those occurring in the “meeting and passing ceremony” described for the Moorhen by Howard (1940).

Appeasement behavior of chicks: Begging.—Day-old Sora chicks begged toward their parents with loud, plaintive peeping calls and gaping. Gaping first consisted of raising the head and neck upward with the mouth open. By the second day after hatching, the chicks pecked at the tip of the parents’ bill. The frequency of pecking appeared to increase as the interval between feedings increased. Pecking appeared to stimulate the brooding parent to call tug. Tug calls may have acted to entice the other parent to bring food to the nest.

“Begging” young crouched on their metatarsi, waved their wings asynchronously, and alternately gaped and bowed so that their bald forehead and scarlet cere faced the adult (Fig. 5). The down on the head was depressed, but there were no striking color changes of the bared skin of the head. Several weeks after they were able to stand on their toes young Soras continued to crouch on their metatarsi while begging. Waving of the wings made the chick conspicuous.

Begging was first observed in Sora chicks after 3 days of age, when they were able to run to the parent bringing food to the nest. Begging movements were observed after the end of the first day in hand-reared Soras. Begging could have occurred earlier in chicks raised by Soras, but these movements could not be seen because the chicks were usually underneath the adult on the nest. This suggests that begging is elicited by the approach of an adult, and may not be necessary to stimulate an adult to bring food. The main function of begging appears to be appeasement, i.e., the inhibiting of attack by the parents because: (1) begging was elicited by the approach of an adult rather than directed toward the adult brooding the young; (2) the Sora chicks performed the begging display at the highest intensity when they were attacked by the parents; (3) the parent Sora attacked its young with increasing frequency when the young began to lose the bright coloration displayed during begging; (4) the harshest attack made by a male was directed toward a juvenile which failed to beg; (5) juveniles continued to beg after they were able to feed themselves; (6) similarity of the body postures of the begging display and of the “hiding crouch” during a nest disturbance suggests that the begging display reflects tendencies both to flee and to stay.

Virginia Rail chicks did not perform a crouch when begging as did Soras. Virginia Rail chicks peeped when adults approached them and pecked at
food in the bill of the adult. After the first day the chicks ran to the approaching adult, occasionally waving their wings, but stood on their toes.

Vocalizations: Vocalizations associated with hostility and alarm.—Both species have a loud "descending call" which appears to function in territorial defense and as contact call between members of a pair.

The Soras descending call was usually 2–3 sec long and consisted of 10–30 notes. The call progressively decreased in pitch, especially the harmonics of the higher frequencies, and it was reminiscent of the "whinny" of a horse (Fig. 6A). The bird's body contracted and the tail flicked up and down during each note. The white undertail coverts were spread laterally, making the tail flicking conspicuous. The bill pointed downward, except during a territorial dispute when the bird faced its opponent.

Soras gave the descending call frequently during spring migration and throughout the breeding season in response to the calls of the Virginia Rails and other Soras, to a variety of loud noises, and to the sound of splashing water. The descending call of paired males elicited a similar call from the female, usually before the male completed his call (Fig. 6B). The female's call was shorter, more variable, and higher in frequency than that of the male. Sometimes the notes are discontinuous and of alternately high and low frequencies which I called "twittering" (Fig. 6C). A female "twittered" whenever a male other than her mate approached, whereupon
her mate chased the intruder. A female Sora gave a softer version when she was unreceptive during a precopulatory chase.

A one- or two-note cry, described as *kee*, *weep*, *kee-you*, and *per-weep*, often preceded a Sora descending call. These cries were also given separately. The *per-weep* was most common during spring migration and has been reported during nocturnal flight (R. Oehlenschlager, pers. comm.). The *per-weep* was not given in the breeding pen, but an aggressive, un-
mated male gave this call frequently after he was isolated in a separate pen.

The descending call of Virginia Rails was usually 1.5–2 sec in length and consisted of 9–12 notes (Fig. 6D). The notes decreased slightly in amplitude and frequency, particularly at the end of the call. The descending call of the female was higher in frequency than that of the male. The call was reminiscent of the raebh of a drake Mallard (Anas platyrhynchos) or the grunt of a pig. The head was held erect during the call, the tail was flicked up and down with each note, and the undertail coverts were spread laterally.

The descending call of Virginia Rails was given in response to other rail calls, loud noises, and the sound of splashing water. The female gave the descending call in response to her mate, beginning to call before the male finished (Fig. 6E). During a bout of duetting the notes tend to become progressively more precisely synchronized. Incubating females often gave single kuk calls, resembling a single note of the descending call. The male immediately responded with the descending call, and the female joined in (after his first or second note) with the descending call.

Territorial males occasionally gave two distinct variants of the typical descending call: one call has a raspy quality, the other has a hollow quality, and its amplitude is greater at lower frequencies. A few observations indicated that the raspy-sounding descending call elicited a descending call from a mate but not from rival males, whereas the rival males gave a descending call in response to a hollow-sounding descending call but the mate did not respond.

A sharp kiu was given when I entered the pen and alarmed the rails. This is a short, high frequency call, with some harmonics reaching 16 kHz (Fig. 6F). The kiu of the Sora and of the Virginia Rail were indistinguishable to my ear. Both species reacted to kiu of either species by sleeking their feathers and flicking their tails up and down.

A short, high frequency call similar to the kiu was given by adults of both species whenever I approached a nest with eggs close to hatching. The members of a pair gave the call alternately, one higher-pitched than the other. Although they called only 1 or 2 m from me, identification of the sexes was difficult because they remained in the densest vegetation and stopped calling if I approached too closely. Glimpses of wild color-marked birds running for cover indicated it was the female which gave the higher pitched call. The alternation of calling is probably responsible for the ventriloquial effect attributed to rails. The calls of the two species were easily distinguishable from each other and from the kiu. The Sora’s call is phonetically rendered as a keep (Fig. 6G) and that of the Virginia Rail’s as a skew.
A variety of "squawks" and "squeals" were given by both species when they were attacked. A sharp *kuc* was occasionally uttered by a Virginia Rail immediately before being chased. A rapid, two-note *cheek-it* was given by young Soras whenever I handled them. This latter call was first heard at 2 days of age and was given for 2 months.

**Calls associated with pair formation, copulation, and nesting.**—The Sora's "spring peeper call" (resembling the call of the spring peeper [*Hyla crucifer]*) has been described as a "mate-attraction" or "readiness-to-pair" call (Brewster 1902, Pospichal and Marshall 1954). I only heard such a call once from a wild bird and once from a captive bird.

The *kadic-kadic* of Virginia Rails is a high frequency call with short double notes (Fig. 6I). I did not hear this call by captive birds, but I often heard it in the wild shortly after this species arrived in my study areas in spring. Brewster (1902) believed this call functioned to attract a mate.

A short, often repeated *tick* was given by adult Virginia Rails in the early stages of pair formation (Fig. 6J). A louder *kick-it* was frequently heard in the wild during the breeding season but not from captive birds (Fig. 6H). The males of two captive pairs of Virginia Rails gave a large number of squawks immediately prior to nesting (Fig. 6K).

Both species gave soft, "peep"-like calls which appeared to function in maintaining contact between the members of a pair. Both "peeps" are short (0.05 sec) but the "peep" of the Sora is higher in pitch than the nasal "peep" of the Virginia Rail (Fig. 6L, M). Most Sora's "peeps" led to meetings, while Virginia Rail's nasal "peeps" appeared to serve as contact notes.

Virginia Rails also uttered several other soft calls for pair contact. A *tipit*, consisting of rapid, soft sounds resembling water dripping, was given in the same situations as nasal "peeps." Occasionally, a bird gave a complete range of intermediate calls, starting with soft *tipits* which became louder nasal "peeps," then loud plaintive "peeps" and eventually became loud "squawks" and "squeals." A soft purring call was frequently given by either sex when they were close together (Fig. 6Q). This "purr" was often associated with bill nibbling.

Calls given by males during a precopulatory chase are soft and low in amplitude and pitch. The Sora's *gwoo* resembles a soft "cooing" (Fig. 6N). It was also occasionally given during swanning displays between males. The Virginia Rail's "growl" resembles the low guttural sounds made by a person's empty stomach. Virginia Rails occasionally gave a "growl" immediately before being attacked.

Both adults of two pairs of captive Soras gave a gargle-like call at the time of nest relief. The incubating bird gave the "gargle" with increasing loudness, pitch and frequency of notes per second until the mate came
and a changeover of birds incubating occurred. The frequency of "gargles" per second increased from 10–22 notes/sec (Fig. 60, P). A third pair of Soras was not heard to call prior to nest relief, nor was the pair of Virginia Rails.

While on the nest, single, short tugs were given by an adult Sora whenever food was brought to it by the mate. The tug sounds like the "gargle" but at a slower rate.

The first calls of rail chicks are soft wheezy "peeps." These calls are given more frequently and are louder and longer when the chicks are cold or hungry. I could not distinguish the wheezy "peeps" of Soras from those of Virginia Rails.

Miscellaneous calls.—A nasal coot-like call was given infrequently by either sex of Soras while feeding. On several occasions a frog-like roock was given by a Virginia Rail. The function of these calls is unknown.

DISCUSSION

The ancestral rallid stock appears to have been a generalized forest-dwelling species which gave rise to Rallus and Porzana (Olson 1973). Both species which I studied have many displays in common. It is not possible to be certain if these displays are similar because of a common ancestry or because of convergent evolution in the marsh habitat.

In contrasting the two species, Soras had a larger repertoire of displays than Virginia Rails. The Soras also performed several displays in a more elaborate and/or ritualized fashion than the homologous (or analogous) displays of Virginia Rails. Swanning was frequently performed by male Soras whereas swanning was rarely performed by male and female Virginia Rails. Social preening seemed stiffer and more ritualized in Soras than in Virginia Rails and in Soras was given before early attempts to copulate. Postcopulatory displays of Soras had a stereotyped form. Members of Sora pairs gave a meeting and passing display upon meeting. Young Soras have more elaborate begging postures reinforced by conspicuous plumage patterns than do Virginia Rails. Members of Sora pairs tended to do more duetting whereas members of Virginia Rails called in both duets and antiphonally.

Many of the differences in these displays are associated with the stronger territorial behavior of Soras. Defense of a well-defined territory plays a greater role in the breeding biology of Soras than Virginia Rails. Soras have evolved more elaborate swanning displays with which to defend their territories. The facial pattern of Soras appears to reinforce frontal threat postures. There may be stronger tendencies of attack and fleeing between members of a pair of Soras as a result of this behavior and coloration. Social preening may be more important in thwarting the aggressiveness
of the male in Soras than in Virginia Rails. Soras appear to avoid facing each other during social preening and quickly turn their heads if they directly face each other. As pair formation ensues and incubation begins, encounters by members of Sora pairs lead to the meet and pass display instead of social preening. Perhaps "meeting and passing" is performed when the tendency to attack the mate is lowered.

SUMMARY

The displays and vocalizations of the Sora (Porzana carolina) and the Virginia Rail (Rallus limicola) were studied at three different sites over a period of 4 years. Many displays and vocalizations are common to both species, but some homologous displays were more elaborate and/or ritualized in the Sora than in the Virginia Rail. In addition, Soras had a larger repertoire of displays. Most notable of these differences were "swanning" displays by male Soras at territorial boundaries, more ritualized preening by Sora mates, performance of the "meeting and passing" display as well as a standard form of the post-copulatory display, and more elaborate begging postures assumed by Sora young. Differences between species may be attributable to the more aggressive, territorial nature of the Sora.

ACKNOWLEDGMENTS

Financial support was provided by the American Association for the Advancement of Science through the Iowa Academy of Science, the Chapman Fund of the American Museum of Natural History, Sigma Xi, and the Wildlife Management Institute. I am indebted to NIH Training Grant 5 TOL GM01779 for financial support during my graduate work.

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LITERATURE CITED


JAMES FORD BELL MUSEUM OF NATURAL HISTORY, UNIV. MINNESOTA, MINNEAPOLIS, MINNESOTA 55455. (PRESENT ADDRESS: DEPT. BIOLOGY, LORAS COLL., DUBUQUE, IOWA 52001.) ACCEPTED 6 JULY 1982.

ANNUAL MEETING

THE WILSON ORNITHOLOGICAL SOCIETY

The Wilson Ornithological Society will hold its 64th Annual Meeting at the University of Wisconsin–Green Bay, 2–5 June 1983.

Scientific program contributions are invited in either lecture-slide or poster format. Abstracts, not exceeding 200 words, must be submitted to Clait E. Braun, Wildlife Research Center, 317 West Prospect Rd., Fort Collins, Colorado 80526 by 15 April 1983.

For additional information concerning the meeting contact Richard Stiehl, Chairman, Local Committee, College of Environmental Sciences, University of Wisconsin, Green Bay, Wisconsin 54302; (414) 462-2272 or 465-2371.
A COMPARISON OF AVIAN FORAGING BEHAVIOR IN UNLOGGED AND LOGGED MIXED-CONIFEROUS FOREST

Kathleen E. Franzreb

Numerous studies have examined foraging behavior in birds (Hartley 1953; MacArthur 1958; Morse 1967a, 1967b; Jackson 1970; Grubb 1975; others). However, little work has been done on determining differences in avian habitat use in modified vs natural environments. To what extent are birds capable of behaviorally compensating for habitat changes? Are some species less affected by habitat alteration than others? The purpose of this investigation was to examine foraging behavior of five avian species in a virgin, mixed-coniferous forest and a recently logged site in the White Mountains, Arizona.

DESCRIPTION OF STUDY AREA

The Willow Creek watershed (131 ha unlogged, 202 ha logged) is located approximately 80 km south of Springerville, in the Apache-Sitgreaves National Forest, Greenlee Co., White Mountains, Arizona. It is a U.S. Forest Service experimental watershed ranging in elevation from 2682–2805 m. The watershed is covered by a mixed-coniferous forest in which Douglas-fir, ponderosa pine, and southwestern white pine are the dominant tree species. A portion of the watershed was logged in 1972 by the selective overstory removal method. Quaking aspen and snags (dead trees) were not removed during timber harvesting. One logged study plot and one unlogged plot, each 15.5 ha and each having approximately the same slope and aspect, were located within 0.6 km of each other. The two plots were selected so that the vegetational components (i.e., tree species composition and densities, and understory vegetation) of the unlogged plot approximated the original vegetation of the logged plot.

MATERIALS AND METHODS

Vegetation analysis.—Within each study plot, vegetation was sampled using the plotless point-quarter method (Cottam and Curtis 1956). The basal area of each tree species was determined using measurements from 400 mature (dbh ≥ 7.6 cm) trees. The volume of live foliage available was determined using integration of standard volume formulas for conical (Douglas-fir, spruces [Picea spp.], and firs [Abies spp.]), cylindrical (pines), and spherical (aspen) tree forms. Specific details on volume determinations may be found in Franzreb (1978). Tree heights were also estimated using a clinometer and then segregated into 3-m height intervals.

Foraging behavior.—Daily foraging observations were collected from mid-May through August 1973 and 1974 while I systematically traversed parallel transect lines. Observations were taken under skies that were clear or less than 30% overcast and wind conditions varied from no wind to light wind (Beaufort scale 0–2). Although data were collected throughout the day, the majority of observations were taken during morning hours (06:00–10:00).

Observations were recorded and analyzed for five species: the Yellow-bellied Sapsucker (Sphyrapicus varius), Mountain Chickadee (Parus gambeli), Ruby-crowned Kinglet (Regulus
**FORAGING BEHAVIOR COMPARISON**

*calendula*), Yellow-rumped Warbler (*Dendroica coronata*), and Gray-headed (=Dark-eyed) Junco (*Junco hyemalis caniceps*). These species were selected because they represent hole, open-cup, and ground nesting species and because they were sufficiently abundant in both study plots to permit vigorous analysis of the data. Data on both sexes were combined since I was primarily interested in species differences between the two habitats and because determination of sex in the field for three of these five species is difficult.

Foraging data were collected for seven niche dimensions: method of prey procurement, substrate character of the foraging surface, perch diameter, distance from branch tip to the perch site, tree species preferred, tree height used, and foraging distance from the ground. One observation (obtained when the bird was first observed) per bird per sighting, was taken to reduce sampling bias.

A Chi-square goodness of fit test was used to compare tree species use to relative frequency of tree species in both plots. The G-statistic (Zar 1974) was used to determine differences in tree species selection between unlogged and logged plots. For this and all other statistical tests, the significance level was defined as $P \leq 0.05$.

For each observation I recorded the height of the tree in which the bird foraged and the foraging distance from the ground. Data were then segregated into 3-m height intervals. Mean values for tree height and foraging height were calculated. The G-statistic was used to compare tree height selection to actual tree height frequency for both plots. A G-test was also used to compare foraging heights in the unlogged and logged areas.

Chi-square contingency tables were developed for plot vs four of the foraging variables (method, substrate, distance from tip, perch diameter) to test for significant differences between the unlogged and logged stands.

Foraging behavior diversity ($H'$) was calculated using Shannon’s (1948) formula. A higher diversity value indicates a species that is more of a generalist with regard to that particular foraging trait. The range in variability in the diversity values was calculated for 95% confidence intervals. Diversity values were tested to determine significant differences ($P \leq 0.05$) using a t-test as described by Hutcheson (1970).

An indication of niche breadth and degree of specialization was estimated by calculating the proportional similarity index (PSI) (Feinsinger et al. 1981) whereby

$$\text{PSI} = 1 - \frac{1}{2} \sum |p_i - q_i|$$

Here $p_i$ is the proportion of resource items in state $i$ of all the items used by members of the species and $q_i$ is the proportion of $i$ items in the resource base available to the birds. This index has an advantage over $H'$ because it relates use to availability and gives a more accurate reflection of the degree of niche specialization. Values range from 0–1 with higher values indicating more generalized behavior in that foraging variable. The PSI was calculated separately for each species and was only determined for those foraging variables for which it was possible to quantify resource availability (tree species, tree height, and foraging height).

Niche overlap was estimated from

$$O_{xy} = 1 - \frac{1}{2} \sum |P_{xi} - P_{yi}|$$

where $P_{xi}$ is the proportion of time spent in resource state $i$ by species $X$ (Schoener 1968); $O_{xy}$ represents the extent of niche overlap between species $x$ and $y$ with total overlap along a dimension yielding a value of 1. Comparisons were made among the three primarily foliage-bark gleaning species (Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler) as it was anticipated that the greatest degree of potential competition existed among them. Overlap results were then tested using the Wilcoxon paired-sample test (Zar 1974) to determine if there were significant differences between the unlogged and logged plots.
Table 1

**Vegetation Analysis of Unlogged and Logged Mixed-Coniferous Forest**

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Tree density (N/ha)</th>
<th>Basal area* (m²/ha)</th>
<th>Foliage vol. (m³/ha)</th>
<th>Relative freq. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>unlog.</td>
<td>log.</td>
<td>unlog.</td>
<td>log.</td>
</tr>
<tr>
<td>Ponderosa pine <em>(Pinus ponderosa)</em></td>
<td>112.7</td>
<td>4.6</td>
<td>16.32</td>
<td>0.81</td>
</tr>
<tr>
<td>Southwestern white pine <em>(P. strobiformis)</em></td>
<td>109.6</td>
<td>8.8</td>
<td>4.98</td>
<td>0.24</td>
</tr>
<tr>
<td>Douglas-fir <em>(Pseudotsuga menziesii)</em></td>
<td>194.1</td>
<td>42.3</td>
<td>17.04</td>
<td>2.29</td>
</tr>
<tr>
<td>Alpine fir <em>(Abies lasiocarpa)</em></td>
<td>3.1</td>
<td>13.0</td>
<td>0.15</td>
<td>0.35</td>
</tr>
<tr>
<td>White fir <em>(A. concolor)</em></td>
<td>51.7</td>
<td>19.7</td>
<td>4.87</td>
<td>0.52</td>
</tr>
<tr>
<td>Blue spruce <em>(Picea pungens)</em></td>
<td>12.5</td>
<td>9.6</td>
<td>0.33</td>
<td>0.16</td>
</tr>
<tr>
<td>Engelmann spruce <em>(P. engelmannii)</em></td>
<td>31.3</td>
<td>19.3</td>
<td>1.20</td>
<td>0.61</td>
</tr>
<tr>
<td>Quaking aspen <em>(Populus tremuloides)</em></td>
<td>50.1</td>
<td>29.3</td>
<td>1.96</td>
<td>1.96</td>
</tr>
<tr>
<td>Snag (dead tree)</td>
<td>61.1</td>
<td>21.0</td>
<td>4.02</td>
<td>2.52</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>626.2</td>
<td>167.7</td>
<td>50.88</td>
<td>9.47</td>
</tr>
</tbody>
</table>

* Trees with dbh (diameter at breast height) ≥ 7.6 cm.

**RESULTS**

_Vegetation analysis._—the logged area had sustained a moderately heavy overstory removal; most of the canopy was eliminated and the original basal area was reduced 83.7% (Gottfried and Jones 1975). Basal area was 50.88 m²/ha in the unlogged area vs 9.47 m²/ha in the logged plot (Table 1). The logged study area had an overall tree density of 167.7 trees/ha including snags vs 626.2 trees/ha for the unharvested plot (Table 1). Basal area and foliage volume (113,984 m³/ha unlogged, 15,270 m³/ha logged) indicated the logged habitat provided a far more open canopy situation with substantially less foliage volume in which to forage in comparison to the unlogged plot. Mean height of live trees was 18.9 m in the unlogged and 12.8 m in the logged plot (Table 2). Additional information on the vegetation is provided in Franzreb (1978) and Franzreb and Ohmart (1978).

_Foraging behavior._—The foraging method of the Yellow-bellied Sapsucker was not significantly different in the study areas (Fig. 1). There was a significant difference ($\chi^2 = 13.43, df = 2, P < 0.005$) in selection
<table>
<thead>
<tr>
<th>Species</th>
<th>Mean tree height (m)</th>
<th>Tree height use vs. available</th>
<th>Tree height use in log.</th>
<th>PSP for tree height</th>
<th>Mean foraging height (m)</th>
<th>PSP for foraging height</th>
</tr>
</thead>
<tbody>
<tr>
<td>YBS</td>
<td>23.4</td>
<td>19.6</td>
<td>**</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>MC</td>
<td>18.9</td>
<td>16.2</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>RCK</td>
<td>20.5</td>
<td>18.1</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>YRW</td>
<td>24.8</td>
<td>18.1</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>GHJ</td>
<td>16.8</td>
<td>11.6</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>Mean tree height</td>
<td>16.4 m</td>
<td>14.4 m</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean live tree height</td>
<td>18.9 m</td>
<td>12.8 m</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**P < 0.01; *** P < 0.001.


G-statistic comparing tree use data to tree height frequency in unlogged and logged plots; all G values ≥ 64, df = 12, all P values < 0.001.

G-statistic comparing use of tree heights in unlogged to use in logged plots; all G values ≥ 43.5, df = 12, all P values < 0.001.

PSP = Proportional similarity index (see text for details).

P value from G-statistic for comparison of foraging height in unlogged vs logged plots; all G values ≥ 30.9 except for YBS.

Including snags.
FIG. 1. Method used during foraging behavior. Open bar represents frequency of class observations in the unlogged area while hatched bar represents those in the logged area. Number at top of each bar is sample size. Bird species are: YBS—Yellow-bellied Sapsucker, MC—Mountain Chickadee, RCK—Ruby-crowned Kinglet, YRW—Yellow-rumped Warbler, GHJ—Gray-headed (=Dark-eyed) Junco. Values less than 1% are not graphed. Chi-square values: YBS ($\chi^2 = 0.61$, df = 3, NS), MC ($\chi^2 = 12.39$, df = 3, $P < 0.01$), RCK ($\chi^2 = 5.94$, df = 3, NS), YRW ($\chi^2 = 3.98$, df = 3, NS), GHJ ($\chi^2 = 9.03$, df = 2, $P < 0.025$).

of foraging substrate between the unlogged and logged plots; the trunk was used more frequently in the unharvested site (Fig. 2). No significant difference was observed in diameter of branches used; larger-diameter branches were selected more often than smaller ones in both study plots.
Franzreb - FORAGING BEHAVIOR COMPARISON

**SUBSTRATE**

1. TRUNK
2. BRANCH/TWIG
3. FOLIAGE
4. CONE
5. MOSS
6. GROUND
7. LOG/SLASH

**SPECIES**

Fig. 2. The foraging substrate from which the bird foraged. Legend follows Fig. 1. Chi-square values: YBS ($\chi^2 = 13.43$, df = 2, $P < 0.005$), MC ($\chi^2 = 47.3$, df = 4, $P < 0.001$), RCK ($\chi^2 = 53.9$, df = 3, $P < 0.001$), YRW ($\chi^2 = 19.7$, df = 4, $P < 0.001$), GHJ ($\chi^2 = 52.5$, df = 5, $P < 0.001$).

(Fig. 3). Sapsuckers did not randomly select tree species but were significantly different in tree species use when compared to availability in both study plots (Table 3, unlogged $\chi^2 = 304.4$, df = 8, $P < 0.001$; logged $\chi^2 = 164.4$, df = 8, $P < 0.001$). Sapsuckers preferentially selected tall trees in both areas although foraging height from the ground was not significantly different (Table 2). For this species foraging differed significantly in the two study sites for substrate, tree species preferences ($G = 75.8$, df = 8, $P < 0.001$), and tree height use ($G = 315.1$, df = 12, $P < 0.001$).
PERCH DIAMETER

1 > 5.1 CM
2 > 2.5 ≤ 5.1 CM
3 > 1.3 ≤ 2.5 CM
4 ≤ 1.3 CM

Fig. 3. Perch diameter selected during foraging. Legend follows Fig. 1. Chi-square values: YBS (χ² = 2.51, df = 3, NS), MC (χ² = 9.38, df = 3, P < 0.025), RCK (χ² = 30.9, df = 3, P < 0.001), YRW (χ² = 11.7, df = 3, P < 0.01), GHJ (χ² = 16.1, df = 3, P < 0.005).

(Table 2). The PSI based on use vs resource availability indicated that sapsuckers were considerably more generalized in tree species selection (Table 3) and tree height use (Table 2) in the logged area.

Significant differences in foraging behavior of Mountain Chickadees were observed for all but the perch diameter variable (Figs. 1–4). Chickadees foraged significantly more frequently near the tips of branches in the unlogged area (Fig. 4) (χ² = 33.8, df = 2, P < 0.01). Greater specialization with respect to tree species selection was evident in the unlogged area (PSI = 0.63 unlogged, 0.77 logged) (Table 3).
Foraging behavior of the Ruby-crowned Kinglet differed significantly between the plots for six foraging variables (all except method) (Figs. 1–4, Table 2). Foliage was the most commonly selected surface on which to forage (Fig. 2). Kinglets relied principally on Engelmann spruce as evidenced by its frequent use (39.2% of observations in the unlogged, 40.8% in the logged) (Table 3). Although mean foraging height appeared similar (10.9 m unlogged, 10.6 m logged), Ruby-crowned Kinglets foraged significantly higher from the ground in the unlogged plot ($G = 30.8, df = 12, P < 0.001$) (Table 2). Kinglets were more specialized in the logged area regarding substrate, tree species use, perch diameter, distance from the tip, and tree height (Tables 2, 3, 4).

In both habitats the Yellow-rumped Warblers principally used Engelmann spruce and Douglas-fir. In the unlogged site ponderosa pine was also frequently used, whereas aspen was selected to a considerable extent in the logged area (Table 3). Yellow-rumped Warblers selected significantly taller trees ($\chi^2 = 152.2, df = 12, P < 0.001$) and foraged significantly higher in the unlogged than logged areas ($\chi^2 = 117.5, df = 11, P < 0.001$) (Table 2). Warblers were much more generalized in the logged area in terms of tree species use (Table 3), tree height preferences (Table 2), and foraging heights (Table 2).

The Gray-headed Junco preferred to forage on the ground or slash (Fig. 2). In the unlogged plot Engelmann spruce was the most frequently used tree species, whereas Douglas-fir was the most commonly visited species in the logged site. Juncos were substantially less generalized in tree species selection in the unlogged area (PSI = 0.60 unlogged, 0.74 logged) (Table 3). Significant differences in foraging behavior were observed between the unlogged and logged plots for all foraging variables except distance from the tip (Figs. 1–4; Tables 2, 3).

Foraging niche overlap was significantly lower in the timber harvested than unlogged plot for the Mountain Chickadee/Ruby-crowned Kinglet (Wilcoxon paired-sample test, $P(T = 0) < 0.02$) (Table 5). Differences between the plots were particularly notable in distance from the tip (Ruby-crowned Kinglet/Yellow-rumped Warbler), foraging substrate (Ruby-crowned Kinglet/Yellow-rumped Warbler), tree species preferences (Mountain Chickadee/Yellow-rumped Warbler), and foraging height (Mountain Chickadee/Yellow-rumped Warbler and Ruby-crowned Kinglet/Yellow-rumped Warbler).

**DISCUSSION**

For many species foraging behavior does not appear to be highly stereotyped or inflexible, and therefore permits a certain degree of accommodation to environmental change. Studies have shown that birds may
### Table 3
Comparison of Tree Species Selection by Foraging Birds in Unlogged and Logged Forests Based on Tree Species Availability, Comparison of Tree Use in Unlogged vs Logged Plots, and Proportional Similarity Indices for Tree Species Use

<table>
<thead>
<tr>
<th>Tree species</th>
<th>YBS</th>
<th>MC</th>
<th>RCK</th>
<th>YRW</th>
<th>GHI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>22</td>
<td>15.5</td>
<td>53</td>
<td>4.7</td>
<td>41</td>
</tr>
<tr>
<td>Southwestern white pine</td>
<td>—</td>
<td>—</td>
<td>94</td>
<td>8.3</td>
<td>53</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>30</td>
<td>21.1</td>
<td>474</td>
<td>42.1</td>
<td>243</td>
</tr>
<tr>
<td>Alpine fir</td>
<td>16</td>
<td>11.3</td>
<td>35</td>
<td>3.1</td>
<td>20</td>
</tr>
<tr>
<td>White fir</td>
<td>6</td>
<td>4.2</td>
<td>152</td>
<td>13.4</td>
<td>58</td>
</tr>
<tr>
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<td>4.9</td>
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<td>61</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>25</td>
<td>17.6</td>
<td>194</td>
<td>17.3</td>
<td>330</td>
</tr>
<tr>
<td>Quaking aspen</td>
<td>10</td>
<td>7.1</td>
<td>66</td>
<td>5.9</td>
<td>34</td>
</tr>
<tr>
<td>Snag</td>
<td>26</td>
<td>18.3</td>
<td>12</td>
<td>1.1</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>142</td>
<td>100.0</td>
<td>1126</td>
<td>100.0</td>
<td>843</td>
</tr>
</tbody>
</table>

χ² value, df: 304.4, 8; 825.8, 8; 2142.2, 8; 466.2, 8; 653.5, 8

P level: *P < 0.001*

PSI:

- YBS: 0.67
- MC: 0.63
- RCK: 0.57
- YRW: 0.78
- GHI: 0.60
### Table 3
**CONTINUED**

<table>
<thead>
<tr>
<th>Tree species</th>
<th>YBS</th>
<th>MC</th>
<th>RCK</th>
<th>YRW</th>
<th>GHJ</th>
</tr>
</thead>
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<tr>
<td></td>
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<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
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<td>20</td>
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<tr>
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<td>19.8</td>
<td>18</td>
<td>2.3</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>668</td>
<td>100.0</td>
<td>771</td>
<td>100.0</td>
<td>730</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>YBS</th>
<th>MC</th>
<th>RCK</th>
<th>YRW</th>
<th>GHJ</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>χ² value</strong> a, df</td>
<td>142.2</td>
<td>8</td>
<td>223.1</td>
<td>8</td>
<td>860.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>P level</strong> b for χ²</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td><strong>PSI</strong> c</td>
<td>0.83</td>
<td>0.77</td>
<td>0.54</td>
<td>0.86</td>
<td>0.74</td>
</tr>
<tr>
<td><strong>G-statistic</strong> d</td>
<td>75.8</td>
<td>197.0</td>
<td>79.8</td>
<td>462.0</td>
<td>58.1</td>
</tr>
<tr>
<td><strong>P level</strong> e for G</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
</tr>
</tbody>
</table>

---

* Based on tree species relative frequency values.
* Species abbreviations follow Table 2.
* Significance level for Chi-square and G-statistic tests $P < 0.05$.
* PSI = Proportional similarity index (see text for details).
* G-statistic comparing tree species use in unlogged vs logged plots.
modify foraging behavior in response to a number of factors such as changes in the structure of the habitat (Grubb 1979) or vegetation composition (Sturman 1968). Szaro and Balda (1980) found that timber harvesting in ponderosa pine forest influenced the behavior pattern of most avian species especially with regard to perch type and tree species selection.

The unlogged habitat presented a vegetation profile of taller trees, with a closed canopy in many places, and a poorly developed understory. Timber harvesting reduced the amount of foraging substrate available for tree
Table 4
Diversity (H'), 95% Confidence Intervals, and Significance Levels for Foraging Variables in Unlogged and Logged Forests

<table>
<thead>
<tr>
<th>Species*</th>
<th>Foraging variable</th>
<th>Method</th>
<th>Substrate</th>
<th>Perch diameter</th>
<th>Distance from tip</th>
</tr>
</thead>
<tbody>
<tr>
<td>YBS</td>
<td>unlogged</td>
<td>0.12 ± 0.13</td>
<td>0.21 ± 0.13</td>
<td>1.13 ± 0.14</td>
<td>0.93 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>logged</td>
<td>0.14 ± 0.14</td>
<td>0.47 ± 0.17</td>
<td>1.25 ± 0.09</td>
<td>1.10 ± 0.04</td>
</tr>
<tr>
<td>SD</td>
<td>NS</td>
<td>t = 2.3, P &lt; 0.02</td>
<td>NS</td>
<td>t = 3.1, P = 0.005</td>
<td></td>
</tr>
<tr>
<td>MC</td>
<td>unlogged</td>
<td>0.19 ± 0.16</td>
<td>0.82 ± 0.16</td>
<td>0.61 ± 0.19</td>
<td>1.04 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>logged</td>
<td>0.14 ± 0.12</td>
<td>0.75 ± 0.17</td>
<td>0.56 ± 0.18</td>
<td>1.02 ± 0.07</td>
</tr>
<tr>
<td>SD</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>RCK</td>
<td>unlogged</td>
<td>0.55 ± 0.15</td>
<td>0.72 ± 0.13</td>
<td>0.66 ± 0.19</td>
<td>1.05 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>logged</td>
<td>0.55 ± 0.13</td>
<td>0.41 ± 0.15</td>
<td>0.44 ± 0.18</td>
<td>0.98 ± 0.10</td>
</tr>
<tr>
<td>SD</td>
<td>NS</td>
<td>t = 3.0, P &lt; 0.01</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>YRW</td>
<td>unlogged</td>
<td>0.39 ± 0.17</td>
<td>0.79 ± 0.14</td>
<td>0.96 ± 0.17</td>
<td>1.02 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>logged</td>
<td>0.39 ± 0.18</td>
<td>0.76 ± 0.14</td>
<td>0.87 ± 0.17</td>
<td>1.06 ± 0.05</td>
</tr>
<tr>
<td>SD</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>GHJ</td>
<td>unlogged</td>
<td>0.05 ± 0.09</td>
<td>1.21 ± 0.13</td>
<td>1.09 ± 0.14</td>
<td>1.08 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>logged</td>
<td>0.17 ± 0.13</td>
<td>1.36 ± 0.09</td>
<td>0.69 ± 0.17</td>
<td>1.09 ± 0.01</td>
</tr>
<tr>
<td>SD</td>
<td>NS</td>
<td>NS</td>
<td>t = 3.5, P &lt; 0.01</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Species abbreviations follow Table 2.

^ t-test as described by Hutcheson (1970).

foragers by drastically decreasing tree density and by removing a substantial proportion of the larger trees (thereby reducing much of the foliage volume and limbs upon which to forage). Reductions along several resource dimensions were apparent in the logged plot including substrate availability, foliage volume, mean tree height, and possibly, food accessibility, quantity, and quality. In addition, there was also an increase in canopy openness as well as an increase in slash and possibly appurtenant changes in insect distributions and densities.

The Yellow-bellied Sapsucker was more generalized in the logged plot in a number of categories such as foraging substrate which may be accounted for by their increased use of branches and foliage. If the logged site was less suitable with regard to nesting and/or foraging either because of reductions in foliage volume or tree densities, one might predict a lower density of sapsuckers there than in the unlogged site. Such was not the case for this species since densities were not significantly different in the two plots during either 1973 or 1974 (Franzreb and Ohmart 1978). The more open habitat (and possibly increased accessibility to prey) and pres-
The differences in larger, more mature aspen in the logged plot (in which the sapsucker constructed its nests) may have been important determinants of its density. Even though densities were similar, there were still a number of significant differences in foraging behavioral categories. These presumably reflect the foraging adaptability of this species, and may have been instrumental in permitting the sapsucker to successfully use the modified habitat.

In the logged plot the Mountain Chickadee shifted its foraging location downward and used shorter trees, thus apparently accommodating to a shift in the overall vegetation structure including the distribution and volume of foliage. In the logged area the chickadee doubled its use of aspen, perhaps reflecting the large amount of aspen foliage available (53.1%) and also its increased relative frequency. Even with this flexibility, the harvested plot supported significantly ($P < 0.05$) fewer Mountain Chickadees than did the unlogged habitat (44.7 birds/40 ha unlogged vs 11.8/40 ha logged in 1973, 58.9/40 ha unlogged vs 30.8/40 ha logged in 1974) (Franzreb and Ohmart 1978).

The Ruby-crowned Kinglet’s relatively high degree of specialization in a number of foraging variables presumably allowed for more efficient exploitation of certain aspects of the logged environment. Kinglets preferred to forage in portions of the trees replete with dense foliage and spent considerable time in the upper portions of trees where the vegetation was

---

**Table 5**

Comparison of Niche Overlap\(^a\) Between Species in Unlogged and Logged Forests

<table>
<thead>
<tr>
<th>Foraging variable</th>
<th>Species compared(^b)</th>
<th>Method</th>
<th>Substrate</th>
<th>Perch diameter</th>
<th>Distance from tip</th>
<th>Tree species</th>
<th>Tree height</th>
<th>Foraging height</th>
<th>Mean overlap</th>
<th>Standard deviation</th>
<th>Difference in mean</th>
<th>$P$ value(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Method</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.83</td>
<td>0.82</td>
<td>0.94</td>
<td>0.93</td>
<td>0.89</td>
<td>0.88</td>
<td>0.97</td>
<td>0.80</td>
</tr>
<tr>
<td>Substrate</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.94</td>
<td>0.86</td>
<td>0.95</td>
<td>0.90</td>
<td>0.97</td>
<td>0.88</td>
<td>0.96</td>
<td>0.77</td>
</tr>
<tr>
<td>Perch diameter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.97</td>
<td>0.92</td>
<td>0.84</td>
<td>0.86</td>
<td>0.86</td>
<td>0.81</td>
<td>0.96</td>
<td>0.77</td>
</tr>
<tr>
<td>Distance from tip</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.97</td>
<td>0.86</td>
<td>0.96</td>
<td>0.90</td>
<td>0.97</td>
<td>0.80</td>
<td>0.96</td>
<td>0.77</td>
</tr>
<tr>
<td>Tree species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.75</td>
<td>0.67</td>
<td>0.73</td>
<td>0.85</td>
<td>0.75</td>
<td>0.83</td>
<td>0.73</td>
<td>0.85</td>
</tr>
<tr>
<td>Tree height</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.81</td>
<td>0.72</td>
<td>0.72</td>
<td>0.80</td>
<td>0.75</td>
<td>0.83</td>
<td>0.72</td>
<td>0.80</td>
</tr>
<tr>
<td>Foraging height</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.86</td>
<td>0.82</td>
<td>0.56</td>
<td>0.85</td>
<td>0.65</td>
<td>0.85</td>
<td>0.81</td>
<td>0.87</td>
</tr>
<tr>
<td>Mean overlap</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.88</td>
<td>0.81</td>
<td>0.81</td>
<td>0.87</td>
<td>0.82</td>
<td>0.80</td>
<td>0.81</td>
<td>0.87</td>
</tr>
<tr>
<td>Standard deviation</td>
<td></td>
<td>0.086</td>
<td>0.087</td>
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<td>0.150</td>
<td>0.002</td>
<td>0.129</td>
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<td>0.07</td>
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<td>0.06</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

\(^\text{a}\) Overlap = $O_{ij} = 1 - \frac{1}{2} \sum |P_{ni} - P_{ni}|$.

\(^\text{b}\) Species abbreviations follow Table 2.

\(^\text{c}\) Wilcoxon paired-sample test; significance level $P < 0.05$. 

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the most dense; this tendency was particularly pronounced in the logged plot. The unaltered habitat provided dense cover in many of the even shorter trees because of the high tree density. Kinglets were most active in Engelmann spruce and Douglas-fir, two of the tree species with the most dense vegetation. Tree species with more open needle/leaf configurations such as ponderosa pine, southwestern white pine, and quaking aspen were even less frequently used in the logged than unlogged habitat. The unlogged plot supported significantly ($P < 0.05$) more Ruby-crowned Kinglets than did the logged plot (71.0/40 ha vs 42.1/40 ha in 1973, 74.4/40 ha vs 23.1/40 ha in 1974) (Franzreb and Ohmart 1978). Even though the kinglet markedly altered its foraging strategy by specializing more with respect to all foraging variables (except method), the logged plot still did not support as high a density. The changes in behavior may have been related to a change in structure of the vegetation profile, particularly to the reduction in tree density and mean tree height, and a decline in both foliage density and volume.

In the logged plot the Yellow-rumped Warbler was much more generalized; the extent of the increase in generalization for specific foraging variables was more obvious than for any other species. This warbler frequently forages in open, less dense foliage, so was not as restricted in its location with respect to needle/leaf density as was, for example, the Ruby-crowned Kinglet; hence, more levels of the vegetation profile were acceptable. This may account for the shift to lower foraging sites in the logged area. Although it still preferred to forage in Engelmann spruce and Douglas-fir, the Yellow-rumped Warbler increased its use of quaking aspen in the logged plot and was more generalized in its overall use of the various tree species. Apparently the warbler was quite behaviorally plastic as indicated by its substantially more generalized behavior in the logged area for a number of foraging variables (tree species, tree height, foraging level) and achieved the highest density of any species in the logged plot. Even so, it had significantly ($P < 0.05$) higher densities in the unlogged than logged plot (131.6/40 ha unlogged vs 100.0/40 ha logged in 1973, 89.8/40 ha vs 76.9/40 ha in 1974) (Franzreb and Ohmart 1978).

Gray-headed Junco densities were significantly ($P < 0.05$) higher in the logged plot (76.3/40 ha logged vs 31.6/40 ha unlogged in 1973, 74.4/40 ha vs 51.3/40 ha in 1974) (Franzreb and Ohmart 1978). This may have resulted from the ground-foraging junco's use of logs and slash that were far more abundant in the timber harvested area, its more generalized use of tree species, and because it is a ground nester.

Although it is difficult to substantiate competition using overlap values (Colwell and Futuyma 1971), such values are indicative of resource dimensions along which competition may take place (Williams and Batzli
1979). Even if species exhibit little overlap in one dimension, substantial competition may still occur. Potential competition may have modified foraging behavior for several species in this study; however, it is difficult to distinguish the direct effects of logging and concomitant reductions in resource availability from either the release from, or initiation of, competitive influences.

Kinglets were quite specialized in tree species use—over 80% of the observations were in Douglas-fir and Engelmann spruce in the logged plot—and partitioned the habitat primarily in this regard with respect to the Yellow-rumped Warbler. In comparing the Ruby-crowned Kinglet and Mountain Chickadee, it was evident that there was less overlap in all variables in the logged area, mainly because the kinglets became significantly ($P < 0.05$) less diverse in a number of foraging variables.

With the removal of the mid- to large-sized trees, the vegetation profile was shifted downward in the logged area; hence, the increased degree of overlap in foraging level and tree height use was predicted. Birds may also have responded in the logged site to the shift in tree species frequencies, reduction in foliage densities, openness of the habitat (Yellow-bellied Sapsucker), and enhanced ground slash abundance (Gray-headed Junco). Reductions in foliage volume and densities of preferred tree species could not be compensated for totally by shifts to more abundant plant resources subsequent to logging. Preferences for certain tree species may reflect variation in insect fauna, abundance or accessibility (Orians 1977) and may occur, in part, because different tree species provide varying amounts and densities of foliage.

In studying foraging behavior in 22 insectivorous birds in a northern hardwood forest, Holmes et al. (1979) suggested that the ability to obtain food may vary with distance from the ground and is influenced by certain physical and chemical characteristics of the plant species, principally those related to foraging substrates, food-seeking methods, and food abundances. They noted that the birds partitioned the habitat by tree species use, foraging substrate, and method. Maurer and Whitmore (1981) in comparing an immature to mature deciduous forest, suggested that differences in foraging were related to altered distribution of resources arising from differences in plant species composition and structure.

This study provides further evidence to suggest that these species partition the habitat by selecting different tree species, substrates, tree heights, and foraging heights, and that the vertical distribution of the vegetation, the foliage density, and the relative frequencies of tree species are of major importance in predicting the response of birds to a logged environment. These factors may influence the distribution and availability of resources
such as food, cover, and nesting substrate, and hence, the number of birds a modified habitat can support. Further work is needed on refining the complex interplay of these factors and the resulting responses of the avifauna.

**SUMMARY**

Foraging behavior of five avian species (Yellow-bellied Sapsucker, Mountain Chickadee, Ruby-crowned Kinglet, Yellow-rumped Warbler, and Gray-headed [=Dark-eyed] Junco) was compared in a recently logged mixed-coniferous forest (selective overstory removal) and a natural forest. The structure and profile of the vegetation in the two forest types differed, with the logged area possessing a different tree-species, foliage-volume distribution, far more open canopy cover, and a greater ground surface complexity resulting from abundant slash (logging debris). In the timber harvested plot, foliage volume, mean tree height, and overall tree density were substantially reduced.

In the logged plot some species responded by reducing foraging heights and using shorter trees. Tree species selection varied significantly ($P < 0.05$) for all avian species when comparing tree species use to tree species availability based on relative frequencies and also when contrasting use in unlogged vs logged areas. The distribution of foliage volume by tree species was considerably different in the two plots. Aspen comprised over 53.1% of the total foliage volume in the logged area vs 5.0% in the unlogged. Use of aspen in the logged plot increased at least twofold for the Yellow-bellied Sapsucker, Mountain Chickadee, and Yellow-rumped Warbler.

In the logged area the increase in degree of generalization for the Yellow-rumped Warbler was more pronounced than for any other species. In contrast, the Ruby-crowned Kinglet was quite stereotyped in its foraging and even more so in the harvested area; this coupled with substantially greater specialization in the warbler, was reflected in a reduction in niche overlap between the kinglet and both the chickadee and Yellow-rumped Warbler in the logged site. The results of this study suggest that changes in foraging behavior such as those observed for tree species selection, foraging substrate, tree height use, and foraging height, reflect a shift in vegetation structure and distribution and/or availability of resources.

**ACKNOWLEDGMENTS**

I am grateful to R. D. Ohmart for his advice and guidance throughout the course of this study. R. P. Balda, D. Patton, and J. Thompson kindly offered ideas that were greatly appreciated. I thank B. Maurer, R. Conner, D. L. Pearson, J. Jackson, R. Pulliam, and W. Laudenslayer for providing useful suggestions for improving the manuscript.

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**LITERATURE CITED**


HABITAT ASSOCIATIONS OF BREEDING BIRDS IN COTTAGE AND NATURAL AREAS OF CENTRAL ONTARIO

KAREN CLARK, DAVID EULER, AND EDWARD ARMSTRONG

Limited information is available about the habitat relationships of forest-breeding birds in central Ontario where, in the last 25 years, increasing cottage development has led to widespread habitat alterations. Several studies have examined avian responses to habitat changes caused by logging (Kilgore 1971, Webb et al. 1977). These areas, however, were allowed to revert to forest succession so the alterations were temporary. Cottage development results in major, long-term habitat alterations: the natural vegetation is changed substantially, although complete removal does not often occur, and undisturbed forest patches are left between lakes. Whitcomb (1977) predicted that regional extinction of avian species would be common with the removal and fragmentation of forests. The species most vulnerable to extinction are neotropical migrants (Whitcomb 1977), the most common breeding species in central Ontario forests.

In managing cottage development along lakeshores it is important to know how avian habitat is changed by human activity. The water/land interface is a unique habitat containing both coniferous and deciduous trees while back-shore areas are largely deciduous. The diversity provided by these areas adds to diversity of the larger vegetation community. Cottage development may reduce the diversity of vegetation over large areas much as agricultural activity has reduced the deciduous forest region into islands of woodlots throughout a sea of agriculture. The goal of this work was to provide managers with a detailed understanding of avian habitat requirements in Ontario in natural and cottage areas, and to determine what variables are important in describing the habitat associations. These results are necessary to develop an index of habitat disturbance that can be used to measure potential changes in avian species composition along lakeshore planned for cottage development.

Based on the conclusion that the configuration of the habitat is a major factor influencing habitat selection in birds (MacArthur and MacArthur 1961, MacArthur et al. 1962, Hilden 1965, Anderson and Shugart 1974), various multi-variate analyses can be used to quantify habitat relationships among species (James 1971, Holmes et al. 1979). These analyses indicate which habitat characteristics vary with the occurrence of each species and allow descriptions of avian habitat associations. Although other studies have used a similar approach, no data exist for birds in the Great Lakes/
St. Lawrence forest region. This work is one part of the larger Lakeshore Capacity Study being conducted by the Ontario government, which is investigating the impact of cottage development on other wildlife species as well.

STUDY AREA

The study was conducted in the Muskoka and Haliburton districts of central Ontario (Fig. 1). The area is comprised primarily of rolling, forested terrain with many lakes and rivers
TABLE 1

VEGETATION VARIABLES USED IN THE ANALYSIS OF NEST-SITES AND SINGING POSTS

<table>
<thead>
<tr>
<th>Mnemonics</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>CANVOL</td>
<td>canopy volume (TVOL × CANHT)/10^a</td>
</tr>
<tr>
<td>TVOL</td>
<td>percent tree volume</td>
</tr>
<tr>
<td>TCOV</td>
<td>tree coverage^a</td>
</tr>
<tr>
<td>CANHT</td>
<td>canopy height</td>
</tr>
<tr>
<td>TIND</td>
<td>number of tree individuals</td>
</tr>
<tr>
<td>TREE 1</td>
<td>number of trees 8–16 cm DBH^a</td>
</tr>
<tr>
<td>TREE 2</td>
<td>number of trees 16.1–24 cm DBH^a</td>
</tr>
<tr>
<td>TREE 3</td>
<td>number of trees 24.1–32 cm DBH^a</td>
</tr>
<tr>
<td>TREE 4</td>
<td>number of trees 32.1–40 cm DBH^a</td>
</tr>
<tr>
<td>TREE 5</td>
<td>number of trees 40.1 + cm DBH^a</td>
</tr>
<tr>
<td>TSP</td>
<td>number of tree species^a</td>
</tr>
<tr>
<td>PCCT</td>
<td>percent conifer composition of the trees^a</td>
</tr>
<tr>
<td>TSNAG</td>
<td>number of tree snags</td>
</tr>
<tr>
<td>SVOL</td>
<td>percent shrub volume</td>
</tr>
<tr>
<td>SCOV</td>
<td>shrub coverage^a</td>
</tr>
<tr>
<td>SHIND</td>
<td>number of shrub individuals</td>
</tr>
<tr>
<td>SHSP</td>
<td>number of shrub species</td>
</tr>
<tr>
<td>PCCSSH</td>
<td>percent conifer composition of the shrubs</td>
</tr>
<tr>
<td>SHSNAG</td>
<td>number of shrub snags</td>
</tr>
<tr>
<td>GVOL</td>
<td>percent ground volume</td>
</tr>
<tr>
<td>GCOV</td>
<td>ground coverage</td>
</tr>
<tr>
<td>FHD</td>
<td>foliage height diversity^b</td>
</tr>
</tbody>
</table>

^a Variables used in the discriminant function analysis.
^b Based on MacArthur and MacArthur (1961).

which have been subjected to varying intensities of cottage development. Some lakes are inaccessible by road, and the vegetation has not been extensively altered. Other lakes are circled by a road, a transmission line right-of-way, and a continuous band of cottages so that much of the natural vegetation has been removed.

The study area is located in the ecotone between the boreal and the eastern deciduous forests. It is characterized by a mixture of white pine (Pinus strobus), balsam fir (Abies balsamea), and eastern hemlock (Tsuga canadensis), particularly along north-facing shorelines. Sugar maple (Acer saccharum) and red maple (A. rubrum) are common along south-facing shorelines, white birch (Betula papyrifera) and white cedar (Thuja occidentalis) within 10 m of shore, and beech (Fagus grandifolia) and yellow birch (Betula lutea) more than 20 m from shore.

METHODS

Seventy-three lakeshore study plots, 100 × 100 m each, were selected to represent a wide range of cottage development and habitat types in the area. The plots ranged from completely undeveloped or natural to areas with the highest density of cottages available, about one cottage per 15 m of shoreline. In 1977 and 1978 singing males were censused by the spot map method (Kendeigh 1944) for 4 h between 05:00 and 11:00. The census was repeated
Table 2
Species and Sample Sizes Used in the Analysis of Nest-sites and Singing Posts and the Corresponding Symbols Used in Figs. 1-4a

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Species</th>
<th>Singing Posts N</th>
<th>Nests N</th>
</tr>
</thead>
<tbody>
<tr>
<td>PHOE</td>
<td>Eastern Phoebe (<em>Sayornis phoebe</em>)</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td>LFLC</td>
<td>Least Flycatcher (<em>Empidonax minimus</em>)</td>
<td>30</td>
<td>6</td>
</tr>
<tr>
<td>EWPE</td>
<td>Eastern Wood Pewee (<em>Contopus virens</em>)</td>
<td>18</td>
<td>—</td>
</tr>
<tr>
<td>ROBN</td>
<td>American Robin (<em>Turdus migratorius</em>)</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>SWTH</td>
<td>Swainson’s Thrush (<em>Catharus ustulata</em>)</td>
<td>21</td>
<td>—</td>
</tr>
<tr>
<td>VEER</td>
<td>Veery (<em>Catharus fuscens</em>)</td>
<td>30</td>
<td>12</td>
</tr>
<tr>
<td>REVI</td>
<td>Red-eyed Vireo (<em>Vireo olivaceus</em>)</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>BWWA</td>
<td>Black-and-White Warbler (<em>Mniotilta varia</em>)</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>YRWA</td>
<td>Yellow-rumped Warbler (<em>Dendroica coronata</em>)</td>
<td>30</td>
<td>5</td>
</tr>
<tr>
<td>BTGR</td>
<td>Black-throated Green Warbler (<em>Dendroica virens</em>)</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>BTBW</td>
<td>Black-throated Blue Warbler (<em>Dendroica caerulescens</em>)</td>
<td>30</td>
<td>6</td>
</tr>
<tr>
<td>BBWA</td>
<td>Blackburnian Warbler (<em>Dendroica fusca</em>)</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>OVBD</td>
<td>Ovenbird (<em>Seiurus aurocapillus</em>)</td>
<td>30</td>
<td>7</td>
</tr>
<tr>
<td>ARMS</td>
<td>American Redstart (<em>Setophaga ruticilla</em>)</td>
<td>—</td>
<td>13</td>
</tr>
<tr>
<td>SOSP</td>
<td>Song Sparrow (<em>Melospiza melodia</em>)</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>WTSP</td>
<td>White-throated Sparrow (<em>Zonotrichia albicollis</em>)</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>RBGB</td>
<td>Rose-breasted Grosbeak (<em>Pheucticus ludovicianus</em>)</td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td>YBSS</td>
<td>Yellow-bellied Sapsucker (<em>Sphyrapicus varius</em>)</td>
<td>—</td>
<td>12</td>
</tr>
<tr>
<td>BWHA</td>
<td>Broad-winged Hawk (<em>Buteo platypterus</em>)</td>
<td>—</td>
<td>9</td>
</tr>
</tbody>
</table>

* Species with a sample size smaller than nine were not used in the DFA.

three times between May 26 and July 20. Locations of any nests within these plots were also recorded.

Table 1 lists 22 vegetation variables which were measured, using a modification of the rangefinder method (Anderson and Shugart 1974), in 0.04-ha circular plots centered either on a singing post of a territorial male or on a nest. Since it was not possible to describe the singing posts of all species (Table 2), the species sampled were chosen to represent the range of available habitat. For 12 species, samples of sufficient size to allow measurements at nest-sites were obtained (Table 2).

Principal component analysis (PCA) (Anderson 1958, Morrison 1967) with varimax rotation was used to obtain ordinations of the species along vegetational gradients. The theory and ecological application of the PCA has been discussed elsewhere (James 1971, Gauch and Whittaker 1972). Although unequal sample sizes among species may weight the data in favor of the over-represented species, it was decided that more information would be lost by either reducing the sample size of all species to the same number as the most poorly represented species or to eliminate those species with smaller numbers. Singing posts and nest-sites were analysed separately. All 22 vegetation variables were used in each analysis. The BMD-P4M (Dixon 1975) computer program was used. An ordination was obtained by plotting the mean factor score for each species on the first three principal component axes.

A stepwise discriminant function analysis (Dixon 1975, BMD-P7M) was used to determine which of the vegetation variables are important in discriminating between species habitat
Table 3

Summary of the Results of the Principal Component Analysis of 22 Vegetation Variables for 16 Breeding Bird Species’ Singing Posts

<table>
<thead>
<tr>
<th>Vegetation variable</th>
<th>Component correlations to original variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( p )</td>
</tr>
<tr>
<td>Canopy volume</td>
<td>0.941</td>
</tr>
<tr>
<td>Percent tree volume</td>
<td>0.868</td>
</tr>
<tr>
<td>Tree coverage</td>
<td>0.841</td>
</tr>
<tr>
<td>Canopy height</td>
<td>0.709</td>
</tr>
<tr>
<td>No. tree individuals</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 8–16 cm DBH</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 16.1–24 cm DBH</td>
<td>0.0</td>
</tr>
<tr>
<td>Tree species</td>
<td>0.0</td>
</tr>
<tr>
<td>Ground volume</td>
<td>0.0</td>
</tr>
<tr>
<td>cover</td>
<td>0.0</td>
</tr>
<tr>
<td>Shrub species</td>
<td>0.0</td>
</tr>
<tr>
<td>individuals</td>
<td>0.0</td>
</tr>
<tr>
<td>volume</td>
<td>0.0</td>
</tr>
<tr>
<td>cover</td>
<td>0.0</td>
</tr>
<tr>
<td>Conifer composition shrubs (%)</td>
<td>0.0</td>
</tr>
<tr>
<td>Conifer composition trees (%)</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 24–32 cm DBH</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 32.1–40 cm DBH</td>
<td>0.285</td>
</tr>
<tr>
<td>Shrub snags</td>
<td>0.0</td>
</tr>
<tr>
<td>Tree snags</td>
<td>0.0</td>
</tr>
<tr>
<td>Foliage height diversity</td>
<td>0.380</td>
</tr>
<tr>
<td>No. trees &gt;40 cm DBH</td>
<td>0.455</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>21.1</td>
</tr>
<tr>
<td>Cumulative % variance explained</td>
<td>21.1</td>
</tr>
</tbody>
</table>

*The rows have been rearranged so that for each successive factor, loadings >0.50 appear first; loadings <0.25 have been replaced by zero.

associations (James 1971). If these variables are the same as those represented as important by the PCA, and the resulting distribution of species along the discriminant function axes are similar to those along the PCA axes, then the habitat variables designated as contributing significantly to variation by both analyses should be good predictors of avian habitat association (Smith 1977, Whitmore 1977, Holmes et al. 1979).

RESULTS

Principal component analysis.—The first three components of the PCA of singing posts explained 45% of the total variance in the data set. Only these three components are treated here since the remaining components each explained substantially smaller amounts of the total variance.

The first principal component for singing posts accounted for 21.1% of the total variance, and was highly correlated with canopy volume, tree
Table 4

Summary of the Results of the Principal Component Analysis of 22 Vegetational Variables for 12 Bird Species' Nest-sites

<table>
<thead>
<tr>
<th>Vegetation variable</th>
<th>Component correlations to original variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Canopy volume</td>
<td>0.913</td>
</tr>
<tr>
<td>Tree volume</td>
<td>0.862</td>
</tr>
<tr>
<td>Tree coverage</td>
<td>0.832</td>
</tr>
<tr>
<td>Canopy height</td>
<td>0.795</td>
</tr>
<tr>
<td>No. trees 32.1–40 cm DBH</td>
<td>0.575</td>
</tr>
<tr>
<td>No. trees &gt;40 cm DBH</td>
<td>0.549</td>
</tr>
<tr>
<td>Foliage height diversity</td>
<td>-0.509</td>
</tr>
<tr>
<td>No. tree individuals</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 8–16 cm DBH</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 16.1–24 cm DBH</td>
<td>0.0</td>
</tr>
<tr>
<td>Ground volume</td>
<td>0.0</td>
</tr>
<tr>
<td>No. shrub individuals</td>
<td>-0.281</td>
</tr>
<tr>
<td>Shrub species</td>
<td>0.0</td>
</tr>
<tr>
<td>Ground cover</td>
<td>0.319</td>
</tr>
<tr>
<td>Shrub volume</td>
<td>0.0</td>
</tr>
<tr>
<td>Shrub snags</td>
<td>0.0</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>0.0</td>
</tr>
<tr>
<td>Conifer composition trees (%)</td>
<td>0.0</td>
</tr>
<tr>
<td>Conifer composition shrubs (%)</td>
<td>0.0</td>
</tr>
<tr>
<td>Tree species</td>
<td>0.0</td>
</tr>
<tr>
<td>Tree snags</td>
<td>0.0</td>
</tr>
<tr>
<td>No. trees 24.1–32 cm DBH</td>
<td>0.422</td>
</tr>
<tr>
<td>% variance explained</td>
<td>26.3</td>
</tr>
<tr>
<td>Cumulative % variance explained</td>
<td>26.3</td>
</tr>
</tbody>
</table>

* The rows have been rearranged so that for each successive factor, loadings >0.50 appear first; loadings <0.25 have been replaced by zero.

volume, tree cover, and canopy height (Table 3). Birds found in mature forests with a dense canopy had high scores on this component. Species found in the open habitats of highly developed areas where most of the large trees had been removed had low values on this component. The second principal component accounted for 13.8% of the total variance, and was highly correlated with number of tree individuals, number of trees (8–16 cm), and number of trees (16–24 cm). Species found in early successional forests where there were many small trees, as along the edge of cottage clearings, had high scores on this component. Intermediate scores on this component coincided with undisturbed mature forests, whereas low scores coincided with open areas and disturbed forest habitats where
most of the trees had been removed. The third component accounted for 10.5% of the total variance, and was highly correlated with ground volume, ground cover, number of shrub species, and number of shrubs. Species associated with high values of this component were found where there was a dense understory, as along forest edges, transmission lines, and road rights-of-way. Species with low scores occurred in mature forest, especially coniferous woods, or where the understory had been cleared.

The results of the PCA of the variables measured at nest-sites were very similar to those at singing posts. The first three principal components included the same variables with slight differences in the order of importance (Table 4). Again, as with the singing posts, the first three components each explained a large portion of the total variance. Overall, the first three components for nest-sites accounted for 51.9% of the total variance.

Using the mean of the factor scores of all individuals of each species, a three-dimensional ordination of the species in habitat space was produced. The axes were described by the eigenvectors associated with the first three principal components. This allowed a visual presentation of
Fig. 3. Representation of the first three axes of the habitat ordination of bird species’ nest-sites. A description of each axis is given in the text.

habitat relationships in which the distance from one species to another was proportional to the difference between them (Isebrands and Crow 1977).

Figures 2 and 3 show the habitat ordination of singing posts and nest-sites, respectively. The axes in both figures are associated with similar habitat characteristics. The first axis corresponds to increasing canopy volume and separates the open country birds from the forest birds. For singing posts, the Ovenbird, Swainson’s Thrush, and Black-throated Green Warbler had high scores on this component, while the Song Sparrow, American Robin, and White-throated Sparrow had very low scores.

The second axis is associated with increasing tree density. For singing posts, the Black-and-White Warbler had the highest score on this axis while the robin had the lowest. For nest-sites, the Least Flycatcher, Black-throated Blue Warbler, and Ovenbird had very high scores while the robin and Eastern Phoebe had low scores.

The third axis is associated with increasing amount of understory. For
singing posts, the Black-throated Blue Warbler and robin scored at the high and low extremes of this component, respectively. For nest-sites, the Black-throated Blue Warbler and Yellow-bellied Sapsucker had very high scores while the Eastern Phoebe and Yellow-rumped Warbler had very low scores.

**Discriminant function analysis.**—The DFA requires that the number of variables not exceed the sample size of the smallest group. To meet this requirement, the number of vegetation variables was reduced to nine (Table 1) and any species with a sample size smaller than nine was eliminated (Table 2). The vegetation variables which were included in the DFA were selected to be indicative of the main habitat types and not to show high correlations with any of the former variables. Because of the high correlations among them, the three smallest size classes and the two larger classes for trees were summed to give a single measure of the number of small and large trees, respectively.

Four variables were chosen by the stepwise DFA to differentiate among singing posts of each species (Table 5). The absolute value of the coefficients indicated the relative contribution of each variable to the respective discriminant function axis. The number of small trees, and to a lesser extent, tree cover and percent conifer composition, were major contributors to the first discriminant function axis. Tree cover and ground volume were the major contributors to the second and third axes, respectively. An ordination of the species’ means along the first three discriminant function axes is shown in Fig. 4.

Shrub cover was the only variable entered in the stepwise DFA of nest-sites. A line graph was drawn to illustrate the ordination of species along this axis (Fig. 5).

**DISCUSSION**

**Important habitat characteristics.**—To understand the effect of cottage development on avian communities it is necessary to know what habitat characteristics are important in determining the distribution of breeding birds and to some extent understand why these habitat characteristics are important. Once these habitat characteristics are identified and the avian species associations with them are known, predictions can be made regarding the effects of habitat disturbances on the avian populations in an area.

The vegetation variables indicated by the PCA to be of great importance in describing the variation in this data set agree closely with similar studies by James (1971), Smith (1977), and Whitmore (1977), even though different avian communities and habitats were studied in each case (Table 6). The first two principal components of our study and Smith’s (1977) both describe habitat variables associated with canopy and tree density. James’
Table 5

Standardized Discriminant Function Coefficients for the First Three Discriminant Functions for 15 Species' Singing Posts

<table>
<thead>
<tr>
<th>Vegetation variable</th>
<th>Discriminant function</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of trees 8–32 cm DBH</td>
<td>-0.0436</td>
</tr>
<tr>
<td>% tree coverage</td>
<td>-0.0410</td>
</tr>
<tr>
<td>Ground volume</td>
<td>-0.0159</td>
</tr>
<tr>
<td>% conifer composition of trees</td>
<td>-0.0383</td>
</tr>
<tr>
<td></td>
<td>0.0168</td>
</tr>
<tr>
<td></td>
<td>-0.0004</td>
</tr>
<tr>
<td></td>
<td>-0.0152</td>
</tr>
<tr>
<td></td>
<td>0.0361</td>
</tr>
<tr>
<td></td>
<td>-0.0226</td>
</tr>
<tr>
<td></td>
<td>-0.0939</td>
</tr>
<tr>
<td></td>
<td>-0.0016</td>
</tr>
</tbody>
</table>

* Variables used in the analysis are indicated in Table 1.

(1971) and Whitmore's (1977) results describe similar vegetation characteristics to our study and Smith's (1977), although there are some differences in the order of importance of variables to each component. This can be attributed to differences in the range of vegetation variables sampled in each study. James (1971) sampled mainly deciduous woods in Arkansas in which there were a large number of tree species with a range of heights. Whitmore (1977) sampled open field and forest in Utah of relatively uniform height and dominated by only two tree species. Smith (1977) sampled a forest moisture gradient in Arkansas along which there was a variety of deciduous tree species. Our study included shoreline with coniferous, mixed, and deciduous forest as well as forest altered by cottage development. The lower proportion of total variance explained in our study and that of Smith's (1977) in contrast to that explained by James (1971) and Whitmore (1977) can be attributed in part to their use of mean values for each vegetation variable for each species, fewer vegetation variables, and their sampling of a more restricted range of habitat types.

In another study in Utah, Whitmore (1975) found the four most important variables selected by the DFA were percent canopy cover, percent shrub density, number of small trees, and percent ground cover. With the exception of percent conifer composition which was not considered in Whitmore's (1975) study, his results are comparable to ours. Canopy cover was also found to be the most important variable in a similar study done in Arkansas by James (1971), although her results differed for other variables.

The close similarity of the PCA for song posts and nest-sites further indicates the importance of canopy volume, tree density, and amount of understory in the distribution of individuals throughout the habitat. This similarity also suggests that these vegetational characteristics may be of general significance with regard to satisfying different habitat requirements of different avian species.
Avian habitat selection is considered to be primarily based on proximate factors involving the general vegetative structure, substrate, and terrain (Holmes et al. 1979, Rotenberry and Wiens 1980). The consistent importance of canopy volume, tree density, and amount of understory in our analyses as well as those of James (1971), Whitmore (1975), and Smith (1977) suggests that these vegetational characteristics may be important in terms of specific search images used by birds for habitat selection. There are several possible reasons why these vegetation variables may be important in predicting avian habitat associations.

The canopy layer is important because it adds vertical structure to the habitat providing another dimension for potential food sources, nest-sites, and shelter from predators and inclement weather (Franzreb 1976, Holmes et al. 1979). Willson (1974) found that the greatest variation in species composition occurred when the canopy layer was added to a habitat. Canopy volume has been shown (Morse 1971) to predict the habitat selection of spruce-dwelling wood warblers (Parulinae). Sturman (1968) found that canopy volume was associated with the relative abundances of two chickadee (Parus spp.) species.

Tree density or the number of small trees may be an important measure...
Fig. 5. Ordination of bird species' nest-sites. This axis describes a gradient of increasing shrub cover.

of relative tree size. Tree size may be important in habitat selection because of preferences of some species for certain trunk diameters and heights for singing posts, foraging, and nest-sites (Morse 1967, 1968; Dickson and Noble 1978).

The effect of vegetation ground volume on species distribution may be explained by Roth's (1976) suggestion that increasing ground and shrub volume results in greater spatial heterogeneity. Coniferous composition may be important as another measure of horizontal structuring of the habitat, since conifers provide both an inner and outer layer for which particular species are specialized (MacArthur 1957). Studies relating species diversity to foliage height diversity (MacArthur 1957) have been inconsis-
tent, which suggests that other factors must influence species distribution (Balda 1969, Kilgore 1971, Stamp 1978, Holmes et al. 1979).

Shrub cover may be important in nest-site selection because it could determine different types of concealment from predators and the amount of protection from inclement weather. Shrub cover has been found by Bertin (1977) to be the single most important factor that distinguishes Wood Thrush *Hylocichla mustelina* from Veery territories. Kilgore (1971) found that removal of the ground and lower shrub layers can result in changes in species composition of these layers but does not affect the canopy layer. Since all species examined except the Broad-winged Hawk were found to nest in the ground or shrub layers, other habitat characteristics could have been important if more canopy nesters had been included.

As Holmes et al. (1979) have recently shown, patterns of avian distribution are also influenced by forest plant species composition. In the man-

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### Table 6
**Comparison of the Results of the Principal Component Analysis with Published Studies**

|        | This study | James 1971<sup>a</sup> | Whitmore 1977<sup>b</sup> | Smith 1977  
|--------|------------|--------------------------|---------------------------|-------------
| PC I   | CANVOL     | TSP                      | GCOV                      | TCOV<sup>b</sup> |
|        | TVOL       | TCOV                     |                           |              |
|        | TCOV       | TREE 2                   |                           |              |
|        | CANHT      | TREE 1                   |                           |              |
|        |            |                          |                           |              |
| PC II  | TIND       | SHIND/4                  | SHIND                     | TREE 2<sup>c</sup> |
|        | TREE 1     |                          |                           |              |
|        | TREE 2     |                          |                           |              |
| % total variance explained by PC I and PC II | 35 | 77.3 | 73.5 | 32.2 |
| No. of bird species | 15 | 46 | 24 | 8 |
| No. of variables | 22 | 10 | 10 | 25 |
| Study area | central Ontario: forests, cottaged lots | Arkansas: forests, wetlands | SW Utah: cotton-wood forest, wetlands, farmland | NW Arkansas: forest moisture gradient |

<sup>a</sup> PCA was performed using the mean of each habitat variable for each species.

<sup>b</sup> This principal component also includes number of post oak <22.9 cm DBH, number of black hickory, number of post oak >22.9 cm DBH.

<sup>c</sup> This principal component also includes number of shagbark hickory, number of beech >22.9 cm DBH.
agement of habitat for a variety of purposes, plant species composition has to be considered in addition to the structural features considered in this study.

Effects of cottage development.—By interpreting the positions of each species along the principal component and discriminant function axes, habitat associations and a species’ response to cottage development can be described. The White-throated Sparrow, Song Sparrow, and American Robin were associated with habitats typified by low canopy volume and tree density, shrubby areas and lawns in highly developed habitats. The White-throated Sparrow, usually considered a boreal forest bird (Kendeigh 1948, Martin 1960) was associated with high coniferous composition and dense understory. Its preference for an open canopy with a well-developed understory makes it well suited to inhabit cottaged lots in coniferous woods where most of the tree layer has been removed. The Song Sparrow was associated with mixed conifer composition and a reduced understory found in cottaged areas where much of the vegetation had been removed. The robin, often found in urban areas (Howell 1942, Young 1955, Howard 1974), was associated with very low ground volume and mixed coniferous composition for its singing posts and similar habitat with low shrub cover for its nest-sites. Its ability to nest on drainpipes and ledges and its preference for open areas for foraging allows the robin to be successful in highly developed areas where most of the natural vegetation has been removed.

The phoebe and Eastern Wood Pewee were associated with slightly higher canopy volume and tree density, features indicative of the periphery of a clearing. Both the phoebe and pewee require an open area for fly-catching (Hespenheide 1971, Kilgore 1971) and some canopy for perching. The phoebe’s preference for low shrub cover and its ability to find nest locations on buildings makes it able to inhabit cottaged lots with small clearings which allow for adjacent nesting and foraging habitat. Hespenheide (1971) classified the pewee as an edge species, since the main criterion for its presence is a discontinuity in the canopy layer in close proximity to open areas for foraging and trees for perches and nest-sites. The pewee could be found on the forest edges of cottage clearing regardless of lot size.

Although the Blackburnian Warbler and Veery belong to different feeding guilds, they were both associated with intermediate canopy volume and slightly less than mean tree density. The Blackburnian Warbler was found in coniferous woods with little understory. It is usually associated with a high canopy for foraging (Griscom and Sprunt 1957, Morse 1976) suggesting that it is found on cottage lots in mature woods where the canopy layer has not been disturbed or in undisturbed forests. The Blackburnian Warbler is negatively affected by even low levels of disturbance
(Webb et al. 1977), probably because this species forages among outer twigs and branches of trees (Holmes et al. 1979).

The singing posts of the Veery were in deciduous woods with a well-developed understory. Nest-sites were associated with intermediate canopy volume, tree density, and very high shrub coverage as found by Bertin (1977) as well. The Veery would be expected to benefit from a pattern of tree removal in mature forests where the understory was not disturbed, resulting in greater shrub cover and development of the understory.

The Black-throated Blue Warbler, Yellow-rumped Warbler, and Red-eyed Vireo were associated with intermediate levels of canopy volume and tree density indicative of selective tree removal in mature woods or of immature woods, which in our study area were usually associated with forest succession on cleared lots. The Black-throated Blue Warbler was found in mixed or deciduous woods with moderate canopy volume and tree density. The Black-throated Blue Warbler requires a greater amount of understory. Webb et al. (1977) found that removal of the tree layer did not change the population density of the Black-throated Blue Warbler which suggests that disturbance of the canopy layer should not affect its nesting habitat. Although the Black-throated Blue Warbler forages among the outer twigs and branches of trees (Holmes et al. 1979), it is capable of using a variety of canopy heights and volumes.

The Yellow-rumped Warbler was associated with mixed woods with some understory. This species has been shown to exhibit a high degree of plasticity in habitat preferences for foraging and nesting (Ficken and Ficken 1967, Morse 1971, Franzreb 1976, Dickson and Noble 1978), and is dependent to some extent on competitive displacement (Morse 1976).

The Red-eyed Vireo was associated with deciduous woods with some understory for singing posts and nest-sites. The Red-eyed Vireo has been found to tolerate varying degrees of tree removal (Webb et al. 1977), since it has been reported in habitats ranging from dense shrub to mature forest (Kendeigh 1948, Rice 1978). Conner and Adkisson (1975) and Adams and Barrett (1975), however, found the Red-eyed Vireo intolerant of tree removal, suggesting that in some areas other factors such as competitive interaction may be important in the habitat selection of this species.

The singing posts of the Rose-breasted Grosbeak were associated with deciduous woods with a dense understory. Nest-sites had a low canopy volume and very high shrub cover typical of immature trees where this species has been noted to nest in other parts of its range (Kendeigh 1946, 1948; Kricher 1973). The preference for high tree density and extensive shrub cover leads the Rose-breasted Grosbeak to inhabit areas where large trees have been removed and the understory has been allowed to develop (Webb et al. 1977, Possardt and Dodge 1978).
The Swainson’s Thrush, Black-throated Green Warbler, and Ovenbird were associated with high canopy volume and intermediate tree density indicative of undisturbed forests. The Swainson’s Thrush was associated with high conifer composition and little understory. There is little information available about the nesting habitat of this species. Its association with mature woods suggests an intolerance of any habitat alteration. Webb et al. (1977), however, found that it was not affected by intense logging. Since the Swainson’s Thrush nests in the shrub layer, habitat alterations affecting this stratum may be more critical to its occurrence.

The Black-throated Green Warbler was associated with coniferous, mature woods with considerable understory. MacArthur (1958) and Morse (1971) noted a high degree of stereotypy in habitat utilization, leading to narrow habitat use for this species. These specialized habitat requirements would explain its limitation to undisturbed coniferous woods (Morse 1976, Webb et al. 1977).

The Ovenbird was associated with mixed woods with little understory, typical of undisturbed mature forests. Several studies have indicated population declines with tree removal (MacClintock et al. 1977, Whitcomb et al. 1977, Conner and Adkisson 1975), although Adams and Barrett (1976) found a population increase. The Ovenbird would be expected to be found near cottaged lots in mature woods if human activity did not disturb this ground nesting species.

The Black-and-White Warbler and Least Flycatcher were associated with high tree density and high canopy volume, typical of an area which had been cleared and allowed to proceed to an early successional forest stage. Although the Black-and-White Warbler is considered to be a deciduous forest bird (Harrison 1975), it was associated with high conifer composition in our study area. Since it is a ground nester, it would not be expected to tolerate extensive human activity. Possardt and Dodge (1978) have shown that disturbance of the understory results in a population decline.

The singing posts and nest-sites of the Least Flycatcher were associated with deciduous woods. The Least Flycatcher is a forest bird found near openings in the canopy (Kendeigh 1948, Breckenridge 1956, Hespenheide 1971). Mature forests subject to selective tree removal to open the canopy should provide favorable habitat, whereas extensive tree removal or reduction of the understory should create unsuitable habitat for this species (Webb et al. 1977, Possardt and Dodge 1978).

The PCA and DFA proved reliable in determining avian habitat relationships and the effects of habitat alterations on avian distributions. The information obtained compared favorably with studies involving extensive, long-term data collection (Bertin 1977, Webb et al. 1977, Rice 1978).
The implications of the results of the DFA and PCA are threefold. First, reasonably accurate measures of species habitat relationships can be obtained by measuring only four habitat characteristics: canopy volume, tree density, shrub coverage, and percent conifer composition. A manager, wanting to understand how the habitat of birds breeding in an area is changed by habitat disturbance, can measure these four habitat characteristics and learn a great deal about the magnitude of the disturbance.

Second, DFA and PCA can be used to establish the importance of separate habitat characteristics in avian habitat associations. The impact of cottage development on breeding birds can then be predicted by measuring how cottage construction changes the vegetation. These effects are dependent on the amount of habitat destruction in building on a cottage lot. For example, a cottager on a deciduous lot who selectively removes only a few trees and leaves the ground or shrub layers intact would encourage Veery nesting in the area but deter Ovenbirds.

Third, since only four habitat characteristics are required to establish avian habitat associations, a simple index of habitat disturbance caused by cottage development can be developed to measure effects on avian communities based on the amount of change in the four habitat characteristics. Although the development of an index of habitat disturbance is not discussed here, it was necessary to establish what variables would be useful in developing the index as well as determining how these habitat variables are related to avian habitat associations.

SUMMARY

Habitat associations of breeding birds in central Ontario were determined by measuring habitat characteristics at singing posts and nest-sites and by using these variables in principal component and stepwise discriminant function analyses. These results were then used as baseline data to predict avian responses to habitat disturbance caused by cottage development. Three habitat variables were important in accounting for large proportions of the total variance in all analyses. These were canopy volume, tree density, and amount of understory. The consistent importance of these variables in our analyses as well as in other published studies suggests that these variables may be significant in avian habitat selection. Coniferous composition was important in the discriminant function analysis, and may be important as another measure of horizontal structuring of habitat. By interpreting the positions of each species along the discriminant function and principal component axes, habitat associations could be described and predictions made regarding the response of a species to habitat disturbance caused by cottage development.

In Muskoka-Haliburton removal of the majority of vegetation around a cottage leaves breeding habitat for Song Sparrows and robins. If some predominately coniferous vegetation is left, White-throated Sparrows will also occur. Phoebes and pewees occur on the periphery of cottage clearings. Selective tree removal while leaving the rest of the vegetation undisturbed would create breeding habitat for Veerys, Black-throated Blue and Yellow-rumped warblers, and Red-eyed Vireos. Cottage lots that have been cleared and allowed to go through natural succession to the immature tree stage would create breeding habitat for Rose-breast-
ed Grosbeaks. Swainson's Thrush, Black-throated Green and Black-and-White warblers probably will not occur near cottages because they are intolerant of vegetation disturbance.

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LITERATURE CITED


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GROWTH, DEVELOPMENT, AND FOOD HABITS OF NESTLING MIMIDS IN SOUTH TEXAS

DAVID H. FISCHER

The growth rates of nesting passerines recently have received considerable study (Ricklefs 1968, 1979; Best 1977; Woolfenden 1978); however, few studies have examined mimids (Mimidae) (but see Rand 1941; Killpack 1970; Ricklefs 1965, 1966). Food habits of nesting mimids are also poorly known (see Bent 1948). In this paper I report on growth, development, and food habits of nesting Curve-billed Thrashers (Toxostoma curvirostre), Long-billed Thrashers (T. longirostre), and Northern Mockingbirds (Mimus polyglottos) in south Texas. Each of these mimids is an abundant resident of the brushlands typical of this region.

METHODS

I studied the breeding ecology of Curve-billed and Long-billed thrashers and mockingbirds during the summers of 1977 and 1978 near Dinero, Live Oak Co., Texas. Two rectangular study areas were selected and the vegetation of each sampled with 25 randomly located line-transects (30.5 m) (Canfield 1941). Botanical nomenclature follows Jones (1975).

Plot A (30.3 ha) supported a dense, often impenetrable chaparral (185.5% cover, overlapping vegetative layers) comprised mostly of the following shrubs: colima (Zanthoxylum fagara), blackbrush acacia (Acacia rigidula), agarito (Berberis trifoliata), brasíl (Condalia hookeri), granjeno (Celtis pallida), and mesquite (Prosopis glandulosa). The remaining cover was formed by trees (19.6%), forbs (25.3%), and grasses (16.9%). Two sides of plot A bounded additional chaparral, and two sides bordered a cleared pasture.

Plot B (69.0 ha) was cleared several years prior to my study. Shrub contributed only 7.6% and trees 2.4% of the total 104.9% cover. Forbs, especially gerardia (Gerardia heterophyla), broom snakeweed (Xanthocephalum sarothrae), and golden aster (Heterotheca latifolia), provided 73.6% of the vegetative cover. The remaining 21.3% was formed by grass. All of the Long-billed Thrasher nests were located in plot A. Most Curve-billed Thrasher and mockingbird nests were found in plot B or along the periphery of plot A (Fischer 1980).

Nests were visited between 12:00 and 16:00 at 2-day intervals. On each visit I recorded the weight and wing chord as well as the tarsometatarsus and bill lengths (culmen-nostril) of each nestling. The stage of feather development was also noted. Day 0 designates the day of hatching. Curve-billed Thrashers were measured through day 9, and Long-billed Thrashers and mockingbirds through day 8. Young disturbed beyond these ages would not remain in the nest when replaced, and prematurely fledged. Curve-billed Thrashers normally fledged on day 13, Long-billed Thrashers on day 12, and mockingbirds on day 10 (Fischer 1980).

Ricklefs (1967) presented a graphical method of fitting equations to growth curves. Following his procedures, I found that the growth of the three mimids was best expressed by the logistic equation:

\[ W_{t0} = A/(1 + e^{-K(t - t_0)}) \]

where \( W_{t0} \) is the weight at age \( t \), \( A \) is the asymptote, \( K \) is the growth rate constant, and \( t_{0} \) is the age at the inflection point \((A/2)\) of the growth curve. The slopes of the growth curves
of the wing (carpometacarpus to wing tip), bill, tarsometatarsus, and weight of each species were compared for significant differences using analysis of covariance (Snedcor and Cochran 1976). Growth rate data from 1977 and 1978 were tested, found not to differ significantly, and combined in the following discussion. The level of significance accepted in this study was $P < 0.05$.

Food samples were collected from nestlings between days 3 and 8 or 9 in 1978 using pipe-cleaner ligatures (Orians 1966). Samples were collected throughout the day and stored in 75% isopropyl alcohol. Later, these were identified to family, and measured volumetrically in a 5-cc calibrated test-tube. The diets of the mimids were compared using Schoener’s (1968) index of overlap: $D = 1 - \frac{1}{2} \sum \left| x_{i,j} - y_{i,j} \right|$ where $x_{i,j}$ and $y_{i,j}$ are the frequencies of the $i^{th}$ category for species X and Y.

Food availability was assessed by collecting 50 samples monthly in 1978. Each sample consisted of sweeping 1 m$^2$ of herbaceous growth 25 times with a net, and collecting all potential prey from 1 m$^2$ of ground surface; items were stored and analyzed as described above for nestling diets. Chi-square analysis (Snedcor and Cochran 1976) was used to compare nestling Curve-billed Thrasher diets with food availability to determine dietary preferences, and to compare the proportions of the major taxa for monthly differences.

**RESULTS AND DISCUSSION**

**General Development**

At hatching, each of the mimids was typically altricial and sparsely covered with grayish-black down (Curve-billed and Long-billed thrashers) or a lighter, smokey-gray down (mockingbird). The internal organs were clearly visible through the translucent skin. The skin pigmentation of both species of thrashers was pinkish-red dorsally and whitish-red ventrally, whereas the skin pigmentation of nestling mockingbirds was orange with no tongue spotting, and the tomia and ricti were yellow.

As nestlings aged, dorsal skin pigmentation darkened to reddish-brown on the thrashers, and to a deep orangish-brown on mockingbirds. Nestlings’ eyes began to open on day 3 (mockingbird) or day 4 (thrashers) and were fully open 1 day later. By day 2, papillae had emerged from all pterylae on each species, and between days 3 and 4, sheaths began to emerge from these. The first sheaths erupted on day 5 (mockingbirds) or day 6 (thrashers) on the lower spinal and ventral tracts. By day 8, most sheaths on all tracts except the capital had shattered, and at fledging, virtually all sheaths had erupted.

**Growth**

*Wing chord.*—The longest primary included in wing chord measurements (primary 7) erupted from the sheath on day 7 for mockingbirds or
day 8 for thrashers. Adult mockingbirds had considerably longer wing chords than either of the two thrashers; however, the growth rates of nestling wing chords of each species were similar (Fig. 1a–c), and not significantly different. By day 8, the wing chord had attained 36.0% ($\bar{x} = 36.7 \pm 4.5$ SE mm, $N = 22$), 41.4% ($\bar{x} = 39.8 \pm 3.9$ mm, $N = 3$), and 34.7% ($\bar{x} = 38.8 \pm 3.5$ mm, $N = 10$) of adult wing lengths of Curve-billed Thrashers ($\bar{x} = 102.1 \pm 4.1$ mm, $N = 31$), Long-billed Thrashers ($\bar{x} = 96.1 \pm 2.9$ mm, $N = 95$), and mockingbirds ($\bar{x} = 111.5 \pm 6.8$ mm, $N = 15$), respectively. None of the young could fly when they left the nest.

Bill and tarsometatarsus.—By day 8 the bill length of nestling mockingbirds had grown to 59.6% ($\bar{x} = 6.5 \pm 0.3$ mm, $N = 10$) of adult length ($\bar{x} = 10.9 \pm 1.3$ mm, $N = 15$), compared to 30.0% ($\bar{x} = 8.2 \pm 0.8$ mm, $N = 22$) for nestling Curve-billed Thrashers (adult $\bar{x} = 27.3 \pm 1.1$ mm, $N = 31$) and 38.2% ($\bar{x} = 8.3 \pm 0.4$ mm, $N = 3$) for nestling Long-billed Thrashers (adult $\bar{x} = 21.7 \pm 0.9$ mm, $N = 95$). This difference was attributable to the much longer bill lengths of adult thrashers when compared with adult mockingbirds, and to a significantly ($F = 27.2$; $df = 2$, 688; $P < 0.01$) greater growth rate of the bill of nestling mockingbirds when compared with the thrashers.

The tarsometatarsus of each mimid developed more rapidly than any other appendage measured (Fig. 1a–c). By day 8, they had attained 80.8% ($\bar{x} = 27.8 \pm 2.6$ mm, $N = 22$), 82.4% ($\bar{x} = 29.4 \pm 4.4$ mm, $N = 3$), and 89.3% ($\bar{x} = 29.9 \pm 1.3$ mm, $N = 10$) of adult lengths of Curve-billed Thrashers ($\bar{x} = 34.4 \pm 1.1$ mm, $N = 31$), Long-billed Thrashers ($\bar{x} = 35.7 \pm 1.2$ mm, $N = 95$), and mockingbirds ($\bar{x} = 33.5 \pm 1.3$ mm, $N = 15$), respectively. The growth rates of the tarsometatarsus of the two thrashers did not differ significantly, but both developed slower ($F = 64.9$; $df = 2$, 688; $P < 0.01$) than the tarsometatarsus of mockingbirds.

Weight.—At hatching, while still wet, Curve-billed Thrashers weighed 5.8% ($\bar{x} = 4.9 \pm 0.4$ g, $N = 24$) of adult weights (Table 1), Long-billed Thrashers 6.2% ($\bar{x} = 4.2$ g, $N = 2$), and mockingbirds 7.5% ($\bar{x} = 3.6 \pm 0.3$, $N = 17$). Weight gain in all three species was rapid and by day 8, the young weighed 49.1%, 55.2%, and 73.0% of adult Curve-billed Thrasher, Long-billed Thrasher, and mockingbird weights, respectively (Fig. 1a–c, Table 1). The growth rate of the thrashers did not differ significantly; however, mockingbirds increased in weight at a greater rate ($F = 91.3$; $df = 2$, 688; $P < 0.01$) than either thrasher.

Using Ricklefs’ (1967) procedures, I calculated the following values for the growth rate equation of each species: $A = 55.6$ g, $t_{(i)} = 5.9$ days, and $K = 0.444$ for the Curve-billed Thrasher, $A = 49.9$ g, $t_{(i)} = 5.9$ days, and $K = 0.443$ for the Long-billed Thrasher, and $A = 39.1$ g, $t_{(i)} = 4.8$ days, and $K = 0.452$ for the mockingbird. The predicted asymptotes ($A$) of Curve-
billed Thrashers and mockingbirds agree closely with the limited number of nestling weights that I have from the final day prior to fledging: Curve-billed Thrasher, $\bar{x} = 53.4 \pm 2.6$ g, $N = 6$; mockingbird, $\bar{x} = 40.4 \pm 2.7$ g, $N = 3$). I have no measurements of Long-billed Thrashers from days 11 or 12. Growth constants for the Curve-billed Thrasher in Arizona were: $A = 55.0$ g, $t_{(i)} = 6.3$ days, and $K = 0.384$ (Ricklefs 1968). I analyzed Killpack’s (1970) weight gain data of the Sage Thrasher (Oreoscoptes montanus) and again found the logistic equation best described the pattern of growth, with constants of $A = 34.1$ g, $t_{(i)} = 4.3$ days, and $K = 0.543$.

The time required to grow from 10% to 90% ($t_{10-90}$) of the asymptote (Ricklefs 1967) of the Curve-billed Thrasher was 9.88 days, that of the Long-billed Thrasher, 9.90 days, that of the mockingbird, 9.70 days, and that of the Sage Thrasher (using Killpack’s 1970 data), 8.05 days. In Arizona, Ricklefs (1968) reported a greater $t_{10-90}$ value, 11.5 days, for the Curve-billed Thrasher, apparently indicating a longer developmental period. Ricklefs (1965) reported starvation within broods in Arizona, indicating perhaps a scarcity of food during the breeding season. Although brood sizes averaged larger in Texas than in Arizona (3.8 vs 3.0), none of the nestlings died from starvation during this study (Fischer 1980).

The ratio (R) of the asymptote to adult weight describes the nestling development at the time of fledging (Ricklefs 1967) and is correlated with the feeding tactics of the adults: species foraging terrestrially have R values less than 0.9 (Ricklefs 1968). I determined R values of 0.65 for Curve-billed Thrashers, 0.73 for Long-billed Thrashers, 0.82 for mockingbirds,
and 0.90 for Sage Thrashers (using Killpack’s data). Ricklefs (1968) reported a similar R value, 0.69, for Curve-billed Thrashers in Arizona. Thus, curve-bills in both Texas and Arizona apparently fledge at similar weights.

**Nestling Food Habits**

*Composition and overlap.*—I collected 433 items (N = 90 nestlings, 32 nests) from nestling Curve-billed Thrashers, 45 items (N = 9 nestlings, 3 nests) from nestling Long-billed Thrashers, and 85 items (N = 56 nestlings, 24 nests) from nestling mockingbirds. Each of the mimids fed their young a diversity of food items (for a complete list see Fischer 1979), almost all of which were terrestrial arthropods. Of these, orthopterans, especially acridids, were the most prevalent items numerically and volumetrically (Table 2). Lepidopteran larvae and Arachnida were important components of the diets of each species, and Coleoptera formed a considerable percentage of nestling Curve-billed Thrasher diet. Berries of agarito and granjeno were fed to young of both thrashers but only after day 7.

The nestling diets of each species overlapped broadly with index values of 0.62 for Curve-billed–Long-billed thrashers, 0.72 for Long-billed Thrasher–mockingbird, and 0.63 for Curve-billed Thrasher–mockingbird. Although the overlap values were considerable, it seems unlikely that

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### Table 2

**Diets of Nestling Curve-billed Thrashers (CBT), Long-billed Thrashers (LBT), and Northern Mockingbirds (MOCK)**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>CBT % N</th>
<th>CBT % V</th>
<th>LBT % N</th>
<th>LBT % V</th>
<th>MOCK % N</th>
<th>MOCK % V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthoptera</td>
<td>60.4</td>
<td>61.0</td>
<td>50.8</td>
<td>72.8</td>
<td>64.3</td>
<td>67.4</td>
</tr>
<tr>
<td>Nymph</td>
<td>34.9</td>
<td>36.6</td>
<td>44.8</td>
<td>60.4</td>
<td>25.6</td>
<td>13.9</td>
</tr>
<tr>
<td>Adult</td>
<td>25.5</td>
<td>24.4</td>
<td>7.1</td>
<td>12.4</td>
<td>38.7</td>
<td>53.5</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>16.4</td>
<td>15.5</td>
<td>4.4</td>
<td>3.7</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>12.4</td>
<td>12.4</td>
<td>12.8</td>
<td>8.8</td>
<td>11.5</td>
<td>14.7</td>
</tr>
<tr>
<td>Larvae</td>
<td>6.4</td>
<td>6.6</td>
<td>10.3</td>
<td>5.9</td>
<td>9.3</td>
<td>10.8</td>
</tr>
<tr>
<td>Pupae</td>
<td>0.2</td>
<td>0.2</td>
<td>2.5</td>
<td>2.9</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Adult</td>
<td>5.5</td>
<td>5.6</td>
<td>0.0</td>
<td>0.0</td>
<td>2.2</td>
<td>3.9</td>
</tr>
<tr>
<td>Other Insecta</td>
<td>0.0</td>
<td>0.0</td>
<td>10.0</td>
<td>4.2</td>
<td>13.2</td>
<td>9.8</td>
</tr>
<tr>
<td>Arachnida</td>
<td>7.0</td>
<td>7.3</td>
<td>8.8</td>
<td>5.7</td>
<td>9.8</td>
<td>7.9</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>0.9</td>
<td>1.0</td>
<td>8.8</td>
<td>2.4</td>
<td>1.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Berries</td>
<td>2.9</td>
<td>2.8</td>
<td>4.4</td>
<td>2.4</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*a Percent of the total items contributed by the respective taxa.
*b Percent of the total volume contributed by the respective taxa.
competition for food would occur during the summer months since arthropods and gastropods were abundant. In addition, the foraging sites and tactics of the adults differed considerably (Bent 1948, Fischer 1980).

Prior to feeding their young, adults of each species usually removed the heavily chitinozed portions of the larger prey. These included the legs of arachnids, and legs, head, and wings of orthopterans and coleopterans. Some very large long-horned grasshoppers (Tettigoniidae) were fragmented and fed to two or more young of a brood. Small prey and all lepidopterans were fed to the young without any apparent processing.

Seasonal distribution of nestling foods.—I compared the monthly diets of nestling Curve-billed Thrashers only, since the sample sizes were small for the other two mimids. The relative importance (proportion) of the major nestling foods changed slightly between May and July (Fig. 2a). Orthopterans significantly ($\chi^2 = 12.6$, df = 2, $P < 0.01$) increased in proportion between May and July (Fig. 2a), and predominated during each month. The proportion of coleopterans significantly ($\chi^2 = 8.9$, df = 2, $P < 0.01$) declined between May and June. None of the other changes in taxa among months was significantly different.

When the diet of nestling Curve-billed Thrashers was compared with...
food availability (Fig. 2b), several trends were evident. Orthopterans were fed in about the same proportion as their availability except in July when they were fed in greater amounts ($\chi^2 = 11.7$, df = 1, $P < 0.01$) than expected. Gastropods, although second only to orthopterans in total availability, were avoided and their contribution to diet was minimal. Lepidopterans and arachnids apparently were taken in about the same quantities as their respective availabilities each month.

CONCLUSIONS

The growth and developmental characteristics of each mimid examined in this and other studies were similar, although there was a trend for the smaller species to develop more rapidly. Mimids as a group, and especially thrashers of the genus Toxostoma, appear to fledge at lower young/adult weights than most other passerines studied so far (Ricklefs 1968). Of the 56 passerine species examined by Ricklefs, only the Horned Lark (Eremophila alpestris) fledged at a lower R value than the Curve-billed Thrasher. Predation pressures were great during both years of this study (Fischer 1980), perhaps favoring a short nestling period with much additional growth delayed until after fledging.

SUMMARY

The growth, development, and food habits of nestling Curve-billed Thrashers (Toxostoma curvirostre), Long-billed Thrashers (T. longirostre), and Northern Mockingbirds (Mimus polyglottos) were studied during the summers of 1977 and 1978 in south Texas. The young of each species were typically altricial. The overall growth rates of Curve-billed and Long-billed thrashers were similar ($K = 0.444$ and $0.443$, respectively) and somewhat slower than the smaller mockingbird ($K = 0.452$) or Sage Thrasher ($K = 0.543$, using Killpack's 1970 data). Nestling mimids fledged at weights lower than those of adults. At fledging, none of the young mimids could fly and the wing chords were much shorter than those of the adults. Bill lengths of each species were also less than adult measurements. The tarsometatarsus of each mimid species grew rapidly and by day 8, it had attained at least 80% of the adult length.

The nestling diets of each species overlapped broadly and were dominated numerically and volumetrically by orthopterans. Other major prey were coleopterans, lepidopterans, and arachnids. The diet of nestling Curve-billed Thrashers changed relatively little between May and July.

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LITERATURE CITED

Fischer • NESTLING MIMIDS IN TEXAS 105


TEXAS A&M UNIVERSITY, COLLEGE STATION, TEXAS 77840. (PRESENT ADDRESS: DEPT. RANGE AND WILDLIFE MANAGEMENT, TEXAS TECH UNIV., LUBBOCK, TEXAS 79409,) ACCEPTED 1 MAY 1981.
THE PLAIN-FRONTED THORNBIRD: NEST CONSTRUCTION, MATERIAL CHOICE, AND NEST DEFENSE BEHAVIOR

BETHY TRENT THOMAS

Some members of the Furnariidae construct elaborate enclosed nests (Hudson 1920, Skutch 1969a); one of the largest nests is that made by the Plain-fronted Thornbird (Phacellodomus rufifrons). Short (1975) gives a map of the range of the Phacellodomus superspecies complex showing two disjunct populations, while Vaurie (1980) shows a map with three disjunct populations. Meyer de Schauensee and Phelps (1978) coined the name Plain-fronted Thornbird for the northern race P. r. inornata because, even in hand, the rufous front of this race is not well-marked. Skutch (1969b, Pts. 1, 2) has given a life history account of the bird in Venezuela. However, his observations were limited to unbanded birds in 5 months of a single season. Herein I confirm and supplement many of Skutch’s (1969b) conclusions and give additional information about the nest, its construction, nest piracy, and attempted nest predation based on 3 and 4 years of observations of banded pairs and their young.

STUDY AREAS AND METHODS

I watched thornbirds at two different Venezuelan sites. One banded pair and their young were followed for 4 years in a scrub and grassland area 30 km south of Caracas at Los Anaucos, Estado Miranda (elev. 550 m). Another banded pair at the same site was observed for less than a year. In the Venezuelan llanos, a savanna, at Fundo Pecuario Masaguaral (Thomas 1979), in Estado Guarico (elev. 63 m) I watched banded territorial birds for 3 years and others for shorter periods. Observations of other thornbirds were also made in both study areas at a number of nests where only one bird or none was marked. The birds were mist-netted and marked by placing plastic color-bands on their legs.

RESULTS

The sexes.—Plain-fronted Thornbirds are monomorphic. Both members of a pair share in all phases of the reproductive cycle, thus the sexes are difficult to distinguish in the field. With prolonged observations of banded pairs, however, I found that one of them did more, or in one case most, of the diurnal incubating and brooding. It was this same bird of each pair that twittered more often in response to its mate’s loud calls, although both are capable of loud calling. I therefore agree with Skutch (1969b) that this bird is probably the female. In the pair which I watched for 4 years I saw one nuptial feeding which further confirmed this assessment of the sexes.
Nests and nest-building.—In the tropical countryside of northern Venezuela one is seldom far from the sight of a thornbird nest. These conspicuous structures are from 0.5–2 m (N = 20) long and the main body has a fairly uniform diameter of 40 cm, not including sticks extending out irregularly from it. Nests are generally suspended from the outer branches of large, isolated trees or on the open side of trees at the edge of deciduous woodlands. Some trees support as many as five nests, or parts of nests, yet in no instance did I ever find more than a single pair of thornbirds and their young occupying a nest tree and its adjacent territory. In color-banded birds of known relationship the extra birds have been the offspring of the territorial pair. Unbanded birds whose relationship to the territorial pair was unknown were occasionally found in the territory.

Thornbirds readily build new nests at any time of year when an occupied nest falls down or when the bottom end, site of the preferred sleeping and breeding chamber, has been usurped by other species of birds. Thus, trees contain old nests and the current nest of the same pair. Vaurie (1980) questioned whether thornbirds use the same nest in succeeding breeding seasons; definitely they do. The thornbird nest is used all year for roosting and I observed three nests 11–13 months after one breeding season in which eggs of the next season were laid. In this respect P. rufifrons differs from several other common Furnariidae, such as Pale-breasted (Synallaxis albescens) and Yellow-throated (Certhiaxis cinnamomea) spinetails, which also build elaborate stick nests but only for one season’s breeding and not for roosting.

Throughout the year thornbirds add to their nests and rearrange sticks on them. When they build a new nest they do most of the work in the early morning hours, with the work gradually diminishing by about 09:30. Occasionally, they build at mid-day and again in late afternoon. When one nest fell during the breeding season it was replaced and eggs laid in less than 3 weeks.

Just prior to egg-laying the pair spends much of the morning vocalizing at the nest. If they are not breeding and the nest is not being used by other species, thornbirds often leave their nest at dawn and do not return until dusk.

The longest thornbird nests are in the llanos (\( \bar{x} = 82.3 \text{ cm}, N = 10 \)), whereas in the tropical areas of the Venezuelan coastal mountains, thornbird nests are shorter (\( \bar{x} = 51.5 \text{ cm}, N = 10 \)). I believe the difference may be related to the abundance of the Trouspial (Icterus icterus) in the llanos (in contrast to the much smaller numbers of Trouspials at higher elevations) because there thornbirds keep adding additional sticks to the tops of Trouspial-pirated nests. Unfortunately, this hypothesis is not easily tested as there is no broad area in Venezuela where the thornbird lives in the ab-
Fig. 1. Plain-fronted Thornbird nest showing successive stages of construction. In cross section E the nest lining is indicated by dotted areas. Arrows indicate entrances to nest chambers.
sence of Troupials, although the reverse is true: Troupials live where there are no thornbirds (Phelps and Phelps 1963).

Thornbird pairs choose their nest-site with much twittering and inspection. On four occasions I observed pairs repeatedly showing interest in certain tree branches even though they already had built a substantial nest. Later, those same branches were used for a replacement nest. After the selection of a site, both members of the pair carry sticks to a place on the chosen branch where there is a forked intersection. Usually the first sticks fall down, or a few may catch, but often wind demolishes the first fragile platform. One pair worked 5 days before their first sticks stayed in place overnight (Fig. 1A). As soon as a platform is established, the birds begin building up the sides to form a steep, conical cup roughly 30 cm across the top and 15 cm deep inside (Fig. 1B). As the cup deepens sticks are laid horizontally across the rim and gradually the center is roofed over as in Fig. 1C. At this stage the birds begin roosting inside and probably also begin to line this first chamber. Even pairs without young continue to build, adding more sticks to the top of the nest to form a second cup, which is roofed over as before. Many thornbird nests have four or more chambers stacked one on top of the other, each with its own entrance, and not interconnected with the others (Fig. 1D,E). Often the upper chambers, which are sometimes lined, are reached through entrances which protrude slightly, like pockets (Fig. 1F). As Skutch (1969b) reported, there is usually an antechamber, or tunnel, leading into each chamber. Most nests are built on outer tree branches which may be bent downward through an arc of 60° or more as the weight of the nest increases. The basic shape of the first conical nest cup, now rotated as in Fig. 1E, can be seen where the back and bottom, including the entrance tunnel, of the lowest chamber preserve the original cup shape.

When the much larger Troupial attacks a nest, it enlarges the lowest chamber by pulling out sticks and nest material to get inside. The thornbird's response is to roost in an upper chamber and to build more chambers on the top of the nest, or to abandon the nest entirely and start a new one. Thornbird nests appear to be very compact, but a flashlight inserted into one at night reveals hundreds of holes. Thus, the nest is probably well ventilated, and the interstices allow the birds inside to see out. This may explain a bird's rapid flight from the nest when a predator approaches (Skutch 1969b, pers. obs.).

Nest materials.—The sticks of nests are so tightly interlaced that a fallen nest can be picked up nearly intact by the stub of the broken branch. I took apart a fallen thornbird nest at Los Anaucos in August 1978. The nest contained three eggs, only one of which was smashed in the well-
lined chamber by the 5 m fall. The nest measured 56 cm in length and 43 cm in diameter and was typical of smaller nests. A pair and two of its young from the previous year had been using it. There were two nest chambers but, as usual, the eggs were in the bottom one, which had an inside diameter of about 12 cm. The nest lining was thinner on the top (2–4 cm) and thicker on the bottom (4–5 cm), as in Fig. 1E.

While taking the nest apart I was careful not to break any of the sticks, which I sorted into five classes by length: 1–10, 10–20, 20–30, 30–40, and over 40 cm; a few sticks less than 1 cm long were not counted. All the sticks were between 1–5 mm in diameter. Each size class was also divided into thorny and non-thorny sticks. A thorny stick was one with thorns sharp enough to pierce my finger easily (Table 1). I separated the breeding chamber lining from the nest structure but did not count the dry grasses which made up its bulk because, after a year as the nightly roost for 2–5 birds, much of the floor had been ground to a fine powder.

Other materials used in both the nest and the lining were of two kinds—natural and man-made. The natural materials were: one dry rolled seed pod, one butterfly wing, two other insect wings, 11 dry bamboo leaves, 13 miscellaneous dry leaves, 19 pieces of roots, 39 thin, papery pieces of bark, and 97 pieces of tree bark. Man-made components included a small piece of paper, a piece of window screening about 5 cm², and more than 160 fragments of thin plastic, each greater than 1 cm². The plastic pieces had not been placed indiscriminately; they generally formed a layer between the sticks of the outer nest and the grass nest-lining.

I found that there were nearly four times as many non-thorny sticks as thorny ones in the nest and that almost twice as many sticks, by weight, were in the 10–20 cm class. The longest thorny and non-thorny sticks were 46.7 and 52.4 cm, respectively. Many of the thorny sticks had 2–4 cm thorns at regular intervals. Intuitively it would seem as though thorny sticks should be more desirable for constructing the tightly linked nest.

**Table 1**

<table>
<thead>
<tr>
<th>Length (cm)</th>
<th>Thorny sticks</th>
<th>Non-thorny sticks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–10</td>
<td>325</td>
<td>1268</td>
</tr>
<tr>
<td>10–20</td>
<td>262</td>
<td>966</td>
</tr>
<tr>
<td>20–30</td>
<td>79</td>
<td>202</td>
</tr>
<tr>
<td>30–40</td>
<td>22</td>
<td>41</td>
</tr>
<tr>
<td>&gt;40</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>698</td>
<td>2484</td>
</tr>
</tbody>
</table>
However, Skutch (1969b) also found that the birds he observed used predominantly non-thorny sticks, and he questioned the justification of the birds’ common name. Were non-thorny sticks preferred by thornbirds, or did this use reflect their abundance in the environment?

Experiments.—When thornbirds build new nests, they transfer sticks from their old nests, whether the nests are still hanging on the tree or fallen below it. Birds even remove sticks from nests still in use for nightly roosting. A series of tests was made to find out the size and type of sticks birds would select when offered carefully matched pairs of sticks of the size (diameter and length) and type (thorny and non-thorny) used in nest-building. I cut dry thorny and non-thorny sticks to experimental lengths from plant species available in territories of the birds. These sticks were placed in identical trays on the ground near a pair building a new nest. Only one kind of test was made on each day, and most tests were made in the first 3 h of the day. At the end of each hour I replaced sticks that were taken, thus beginning a new test each hour. I combined test results as there was no evidence that choice differed with the hour or the nest-building stage (Table 2).

I watched the birds make selections which appeared to be a matter of choice. Once a bird found a tray, its mate quickly followed. Both birds

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**Table 2**

<table>
<thead>
<tr>
<th>Stick Choice Experiments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Thorny (10–20 cm)</strong></td>
</tr>
<tr>
<td>Sticks taken</td>
</tr>
<tr>
<td>41</td>
</tr>
</tbody>
</table>

Test 1. Four trays with five matching sticks of each category, total stick-hours of each type offered, 300; Los Anaucos 15 h on 4 days combined.

<table>
<thead>
<tr>
<th><strong>Short (10 cm)</strong></th>
<th><strong>Long (20–30 cm)</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sticks taken</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>15</td>
</tr>
</tbody>
</table>

Test 2. Four trays each with five matching sticks of two size-classes all non-thorny, total stick-hours of each size offered, 80; Los Anaucos 4 h on 2 days combined.

<table>
<thead>
<tr>
<th>Length in cm</th>
<th>Thorny</th>
<th>Non-thorny</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>20</td>
<td>30</td>
<td>12</td>
</tr>
<tr>
<td>30</td>
<td>36</td>
<td>6</td>
</tr>
</tbody>
</table>

Test 3. Four trays each with 12 matched sticks, two sticks of each size and of each type, total stick-hours for each size and type, 160; Los Anaucos 20 h on 8 days combined.

<table>
<thead>
<tr>
<th>Sticks taken</th>
<th>9</th>
<th>7</th>
<th>7</th>
<th>2</th>
<th>1</th>
<th>0</th>
</tr>
</thead>
</table>

Test 4. One tray with 12 matched sticks as in test 3, total stick-hours for each size and type, 52; Masaguaral 26 h on 6 days combined.
flew from their nest directly to the edge of the tray or landed beside it. A bird paused, looked at the sticks, then hopped up to and picked up a stick at the mid-point with its bill. Occasionally a bird discarded the first stick chosen and selected a different one instead. Then the bird flew with the stick back to its nest, often flying to successively higher branches as described by Skutch (1969b). As most tests were made with the same pair of Los Anaucos birds, I also tested a pair of birds at Masaguaral. Although I have fewer data from the latter, the results are essentially the same.

When offered a choice thornbirds selected more thorny than non-thorny, and generally longer than shorter sticks. Therefore, it might be that sticks of preferred attributes are limited in the habitats that I studied. Collias (1964) suggested that thorns deter predators as Skutch (1969b) and I both learned when we tried unsuccessfully to insert our hands into nest chambers.

Contributions to nest building by ‘helpers.’—The morning after a wind storm destroyed the bottom half of a Los Anaucos nest, the principal pair began to construct a new nest on the same branch, but at a fork below the part of the nest still intact. That night the adults and their three young (about four months old) spent the night in the upper section. (Young spent up to 16 months roosting in the nest.) Each day the pair spent much of the morning working on and calling from the new nest. They transported most of the sticks from the upper section to the new nest and by the sixth night all five birds roosted in the new nest. During 354 min of observation on five different days the male brought 112 (53.6%) of the sticks, the female 69 (33.0%) and two of the three young helped by bringing 17 (8.1%). However, the young birds primarily contributed 2–4 cm pieces of nest-lining. Eleven (5.3%) sticks were brought by unidentified birds.

What happens to nests?—In 57 months the Los Anaucos pair built 12 complete nests and laid small foundations for four others that were never completed. The events which made replacement nests necessary were: (1) six times the nest-supporting branch broke off; (2) once wind tore out the bottom half of a nest; (3) twice the entire half of a nest tree collapsed; and (4) twice the nest was abandoned (once after predation and once because of Troupial interference). However, this pair fledged eight young in four breeding seasons. At Masaguaral, where the Troupial is especially abundant, nests were more often lost because of piracy by this icterine. In 45 months in one territory six nests were built: five were lost to Troupials and one to wind. One other nest was started but not completed.

Interactions with Troupials.—Skutch (1969b) outlined the manner in which a Troupial takes over the lower, principal chamber of the nest. At Masaguaral several times I found two Troupials roosting in a single thorn-
bird nest, but in separate holes. They use nests for breeding and also roost in them all year.

Troupials are not secretive about their piracy. They call near a nest and often begin take-over by vigorously pulling out sticks. One bird at Masaguara1 tore at a nest and dropped the sticks on the ground below. If a stick it pulled out caught in the bottom of the nest the Troupial removed it again, even leaning far over backwards to make sure the stick fell to the ground. In 15 min the bird removed 47 sticks, tearing out about six sticks at a time, which were dropped directly below the nest, and then carrying the next stick 2–6 m away from the nest. Sightings that are occasionally reported of Troupials carrying sticks may be a result of this type of behavior rather than nest construction. Commonly, when a Troupial takes over the bottom chamber of a thornbird nest, it also removes some sticks from above that chamber which gives the nest a profile resembling a narrow-waisted wasp (Fig. 1F). At this point the nest sometimes gradually separates and occasionally thornbirds breed in the bottom part of the upper section as though it was totally independent of the rest of the nest.

Skutch (1969b) made no mention of nest defense by thornbirds, but I saw thornbirds ($\bar{x}$ weight = 24 g, $N = 31$; see Thomas 1982) defend nests against Troupials ($\bar{x}$ weight = 68 g, $N = 4$; see Thomas 1982) on a number of occasions. On the morning of 5 July 1978, a Troupial, although rare in the area, found the Los Anauocos study nest and called from the top of the nest tree. It returned in the late afternoon of the same day and began tearing out sticks from the bottom. The thornbird pair was very excited, calling and hopping about on the top and back side of their nest; their vocalizations attracted one of their 10.5 month-old young. Then the Troupial froze motionless for 9 min, its feathers tightly sleeked, while clinging to the entrance of the lower chamber of the nest. Finally, at 19:05, the Troupial forced its way inside. Ten min later the thornbirds went quietly to roost in an upper chamber of the nest.

The following day the Troupial called, often from near the nest. However, that evening the thornbird pair and their two yearlings entered the remodeled lower chamber before the Troupial. Four min later the Troupial entered the same hole causing three of the four thornbirds to fly out in alarm, but the male thornbird remained, clinging upside down to some sticks below the entrance hole. The Troupial perched above it in the enlarged entrance and jabbed its bill down into the thornbird’s abdomen. The thornbird lost a number of feathers before it flew away. After that the Troupial pulled out more nest material and then moved inside. Then the male thornbird returned to the lower chamber entrance and, joined by another thornbird, twittered excitedly. This thornbird suffered no permanent injury.
At Masaguaraal two Troupials had been roosting nightly, for more than a month, in the bottoms of two adjacent thornbird nests. The thornbirds were building on the top of the newer nest, taking sticks from the older one 1 m distant. On 23 May 1980 I watched the banded female of the pair while she added sticks to the top of the nest. A stick dropped and she darted down after it over the side of her meter-long nest, but stopped at the large Troupial hole at the bottom, which she entered. Instantly a Troupial, which I had not previously noticed, flew in after her. The thornbird uttered a distress "scream," unlike any call I had ever heard from a thornbird. The sound quickly attracted birds of six species to the vicinity of the nest, including a second Troupial which also flew into the same hole. At this point the thornbird flew out, pursued by a Troupial. This thornbird was not seen again. Five days later its mate appeared to be mated with an unbanded individual.

Parasitism.—Skutch (1969b) cited a report that thornbird nests are parasitized by Striped Cuckoos (Tapera naevia). On 30 September 1977, at Masaguaraal, I found a large, loudly begging fledgling Striped Cuckoo being attended and fed by a pair of thornbirds. The cuckoo was about 2.5 times the size of its foster parents.

Nest predation.—Nestling thornbirds are extremely vocal, behavior unusual for tropical nestlings, which may make them obvious to predators. At a Masaguaraal nest I observed a predation attempt. Tropical nest predation is common (Ricklefs 1969) but because it is seldom observed, I have included the following account of the birds’ behavior paraphrased from my field notes. On 12 August 1981, I was watching a thornbird nest at which the banded adults were feeding noisy nestlings:

17:35—A Ferruginous Pygmy-Owl (Glaucidium brasilianum) flew from a wooded area to a tree about 15 m from the thornbird nest, landing at nearly the same height as the nest, and perched motionless in the crotch of an upright branch.

17:36—The female thornbird returned to the nest with food in her bill, but she paused momentarily on the nest before going to the nest hole to feed her begging young. She saw the owl and instantly dropped the food she was carrying and flew toward the owl uttering a chipping call. As she reached a branch 7 m from the owl, she was joined by the male thornbird, who also chipped. They faced the owl and moving to within 2 m of it, they continued to call. A Rusty-margined Flycatcher (Myioborus cayennensis), attracted by the thornbird chipping, flew to a nearby branch and called; other birds gathered overhead.
17:40—The owl flew back into the woods with several birds, including the thornbirds, in pursuit.

17:52—The female thornbird returned to the nest and fed the nestlings.

18:13—Chipping heard again.

18:14—The owl returned to the same tree as before but perched on a different branch, 2 m closer to the thornbird nest. The female thornbird chipped from about 4 m above the owl. Abruptly she stopped and darted into the nest hole with her nestlings. The male thornbird also returned to the nest and quickly entered the same hole.

18:16—The thornbirds were silent.

18:19—The owl flew to a branch of the nest tree and then onto the nest. Twice it went into an empty hole near the top of the nest. Then it perched on a branch 2 m away and looked (probably listened) toward the nest.

18:20—The owl flew back to the nest and directly to the correct (lower) nest hole, which was visually less conspicuous than the first hole it had tried. The owl went into the nest tunnel several times. It was far enough inside that only the end of its tail was visible, but each time it withdrew, apparently because it was repulsed by the adult thornbirds within. No sound was audible from where I sat at 20 m distance.

18:22—The owl then flew to a different branch in the nest tree, slightly below the level of the nest hole and about 2.5 m away and faced the nest.

18:31—An unbanded thornbird which had been roosting each night in a third hole, on the upper side of the nest, flew directly and silently to its hole, as it had done on the previous night. From the direction the thornbird came, it may well have been unaware of the waiting owl.

18:46—The owl turned away from the thornbird nest and flew into the woods.

18:50—A second unbanded thornbird came to roost, cheeping noisily, pausing as it had on the previous night in a bush directly below where the owl had last perched. Then it flew, still cheeping, to join the other unbanded thornbird for the night.

CONCLUDING REMARKS

Using the nest that I took apart as a measure, I estimated that a 2 m-long nest contains approximately 11,384 sticks and has a probable dry
weight of about 7.22 kg, or 300 times heavier than the weight of the birds that built it.

Thornbird nests appear to be energetically expensive. Nest-building and care is done mostly by the territorial pair with the male apparently being the principal builder. The young, which roost in the nest up to 16 months of age, occasionally bring nest-lining material and a few sticks. Young do adjust sticks on the exterior of the nest but their contribution to building and maintenance is minimal.

One possible advantage of thornbird sociality might be defense of the territory by the young against conspecifics, particularly when the principals are occupied with the long breeding sequence (incubation 16–17 days, nestling period 21–22 days [Skutch 1969b]). During territorial disputes as many as seven thornbirds gather and call defensively. In my observation of one Troupial attack, a young bird did join its parents in nest defense, but no other thornbirds responded to the predation attempt by the pygmy-owl.

**SUMMARY**

Pairs of Plain-fronted Thornbirds (*Phacellodomus rufifrons*) maintain permanent territories and construct elaborate stick nests for breeding and for roosting throughout the year. Nest material was examined and measurements were made of the size and type of sticks used in one nest. Experiments showed that thornbirds, when given a choice, preferred long, thorny sticks, even though long, thorny sticks were not in the majority by either number or weight in the nest examined. The method of nest construction is described. Thornbird young continue to roost in the nest up to 16 months of age, and they occasionally bring sticks and lining material, but their contribution to nest-building and maintenance is minimal. Nest piracy by the Troupial (*Icterus icterus*) is described as is an apparent nest predation attempt by the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*).

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


Thomas • PLAIN-FRONTED THORNBIRD NEST


The Chihuahuan Desert Research Institute and Sul Ross State University announce the second Chihuahuan Desert Symposium to be held in Alpine, Texas, 20–21 Oct. For information on session topics and submittal of abstracts write Dennie Miller, Cdri, Box 1334, Alpine, TX 79830.
GENERAL NOTES

Pair formation behavior of the Galapagos Lava Heron.—The Lava Heron (Butorides striatus sundevalli) is a small ardeid endemic to the Galapagos Islands (Harris, Birds of Galapagos, Collins, London, England, 1974). This heron is characterized by its dark plumage and rather sedentary habits (Hancock and Elliott, The Herons of the World, London Editions, London, England, 1978). The birds occur along lava rock shorelines in the Galapagos, where they occupy permanent territories containing their nest-sites (Snow, Living Bird 13:15-72, 1975). This heron’s breeding behavior is poorly known. In the only previous study of this species, Snow (1975) noted several differences between Lava and Green-backed herons (B. s. virescens), and she did not observe several pair bonding behaviors typical of herons. These findings suggested that the breeding behavior of the Lava Heron might be atypical compared to other populations of B. striatus.

During a study of Lava Heron territoriality, I was able to examine some aspects of pair formation. Although the study period was short, I observed a number of displays and followed one pair through courtship. In this paper I compare the pair formation behaviors of Lava Herons with those of Green-backed Herons and with the observations of Snow (1975). I especially consider how the sedentary habits and the permanent residency of this bird might have influenced the development of various courtship displays.

Study sites and methods.—My study was conducted on three sites in the Galapagos Islands in December 1978 and January 1979: Academy Bay on Isla Santa Cruz (14 days), James Bay on Isla Santiago (10 days), and Cartago Bay on Isla Isabella (2 days). The study site on Academy Bay encompassed the 1963 study area of Snow. I obtained information on 15 different birds nesting or engaged in pair formation. Most information on pair formation behavior came from the James Bay study site where I watched the courtship of four birds and followed one nestling attempt from the solo male stage into the incubation stage. Most of my detailed descriptions are from this pair but their behavior was typical of other observations I made. I usually watched from a distance of 5-10 m, but at times I approached as close as 2 m with no discernible effect on the birds. Individual birds were recognizable by unique plumage characteristics. I use the behavioral nomenclature developed for the Green-backed Heron by Meyerriecks (Publ. Nuttall Ornith. Club 9, 1960) as modified by Mock (Wilson Bull. 88:185-230, 1976).

Results.—Soft part coloration.—The legs of the Lava Heron turned from gray to a reddish-orange prior to pair formation, as noted by Snow (1975) who found that color changes in males occurred several weeks before egg-laying by the female. By the time of pair formation, the lores turned from green to bright cobalt blue, more so in the male than the female. The bill turned shiny black in males but remained silver-gray in females. In comparison, the tarsi of both the Green-backed Heron and the Striated Heron (B. s. striatus) turn from orange to orange-red, and the lores of the Green-backed Heron turn to blue-black (Meyerriecks 1960; Haverschmidt, Birds of Surinam, Oliver and Boyd, Edinburgh, Scotland, 1968). As with B. s. striatus and B. s. virescens (Meyerriecks 1960), it appears that the male B. s. sundevalli acquired more intense soft-part coloration than the female.

The overall plumage of Galapagos Butorides ranges from a condition similar to mainland B. s. striatus to a condition typical of dark B. s. sundevalli (Harris, Condor 75:265-278, 1973). Snow (1975) noted that a narrow streak on the lores periodically turned yellow and reported that one male lost his streak during incubation. My observations support Snow’s (1975) contention that the yellow streak is a B. s. striatus characteristic. However, I detected no temporal change in the brightness of the streak in individual birds. Snow (pers. comm.)
has indicated that she now believes the yellow streak was lost because of the change in lore color.

Timing of nesting.—Lava Herons can nest three times yearly (Snow 1975). At Academy Bay, six of seven individuals under observation had been recently or were currently engaged in nesting activities. Fledged young were present in one territory, and eggs were being incubated at two other sites. At James Bay I saw no evidence of nesting activity from 23–28 December, but within the next week five birds on adjacent territories assumed breeding coloration and initiated pair formation, soon after heavy rains broke the seasonal drought. Thus, it appeared that the birds on James Bay were more synchronized than those at Academy Bay and that the beginning of the rains on this drier shore may have influenced the start of breeding activity. Similarly, Grant and Boag (Auk 97:227–244, 1980) found rainfall patterns affected the reproductive cycles of Darwin’s finches (Geospizinae) on the Galapagos.

Flight displays.—Snow (1975) suggested that Lava Herons did not use flight displays often. However, I saw many instances of the flight displays described by Meyerriecks (1960) and Mock (1976). I observed “flying around behavior,” “pursuit flights” directed against both adults and older juveniles, and one “supplanting flight” of a male directed against its eventual mate. Birds also flew in “circle flights,” but they did not land at the same place as they started. Similar flight behaviors seem to occur outside of the nesting period and so may be primarily functional in defending or advertising territories.

Pair formation.—Males vocalized from their nest-sites using show calls. The Green-backed Heron gives this advertisement call in the same context. In contrast, however, the Lava Heron also gave shows from its feeding territory during the pair-formation period, occasionally interrupting feeding with such calling. Only skuk-skuk calls were given in agonistic encounters. Vocalizing appears to function in pair formation. In my most complete set of observations, a female approached two advertising males that called on adjacent territories before choosing one of them. These observations differ from those of Snow (1975) who found that the advertising call was rare.

I saw initial pairing of two birds on James Bay. The male advertised with show calls while walking near a bush containing an old nest platform along the landward edge of the lava shore. The male flew out of its territory in a circle flight and then returned, and called from the bush that later held the nest. When its eventual future mate landed nearby, the male flew from the bush and landed near her on the shore. The male then flew back to the bush, and the female followed slowly after him and walked into the bush. Once in the bush, the two began mutual courtship displays. This early pairing sequence resembled that described by Meyerriecks (1960) for B. s. virescens, except for the extensive walking of Lava Herons. Green-backed Herons typically fly to and from their nest locations (Meyerriecks 1960), even though these may be located no higher than Lava Herons’ nests.

In the bush, the male displayed from an old nest platform, performing typical “stretches” and “snaps,” resembling those Meyerriecks (1960) described for B. s. virescens, except I noted no exaggerated swaying during the stretch. As in B. s. virescens, the male’s stretch was often accompanied by a soft coo. The snap was often a gentle “bow” with no bill-snap component characteristic of B. s. virescens. The female initially remained about 1 m from the male, giving stretches and snaps, including the bow. During stretch performances, the female uttered a soft cou. The female display frequency exceeded that of the male, who manipulated old nest material with his bill. Both birds infrequently gave “forwards” and poked each other with their bills. The female stepped onto the nest, carefully positioning herself under the male’s neck, and began to manipulate nest material. Both then manipulated the material before the male moved off to collect new sticks. When together at the nest, both gave snaps and engaged in considerable preening, primarily directed to wings, breast, and back. Allo-
preening involved the female nibbling at the male’s crest. The frequency, extent, and appearance of preening suggested that preening was part of the display repertoire.

The behavior of the female Lava Heron differed in detail from that described by Meyerriecks (1960) for B. s. wisconsin. He noted that, except for nest exchange, stretches were given by the female only after she had gained access to the nest, at which time the male’s stretch display ceased. I saw courting Lava Herons giving simultaneous stretches, before the female had first moved onto the nest-site. Meyerriecks (1960) did not see a female Green-backed Heron perform a snap display, whereas I saw both snaps and bowing in Lava Herons. One time a male mounted a female away from the nest-site. Copulation attempts were not necessarily preceded by stretches and appeared rather casual.

Discussion.—Pair formation of the Lava Heron generally resembled that of the Green-backed Heron described by Meyerriecks (1960). The substantial similarities are added evidence of a close relationship and lend no support for doubting Payne’s (Bull. Br. Ornithol. Club 94:81–88, 1974) view of the conspecificity of the three forms of Butorides.

The ways in which courtship behaviors of Lava Herons do differ from those of Green-backed Herons are of particular interest in that such differences seem to be related to the Lava Heron’s territorial system. Meyerriecks (1960) found that the area defended by the male Green-backed Heron decreased during the period of pair formation. In contrast, a Lava Heron continued to defend a length of shore including its nest-site during nesting, because the nest-site is only part of a larger pre-existing defended area. The protracted maintenance of a large territory may be related to other unusual aspects of pair formation, including the Lava Heron’s reliance on terrestrial rather than aerial locomotion. Also, the courtship activity of Lava Herons is not confined to the nest-site. Males advertise, flights are initiated, and females may make contact with displaying males on the feeding territory away from the nest-site. Expansion of the courtship display arena appears to be a secondary response to the permanent, exclusive possession of a larger land area.

Differences between Lava and Green-backed herons in pair formation displays included the female performing the stretch at the nest-site, her performing snaps, and her lack of swaying. It is possible, however, that such variations also occur in other Butorides populations which are poorly known. My observations may not even reflect the situation in all Lava Herons. My study concentrated on birds that foraged along the lave shore. Other birds nest in mangrove patches and may not have nest-sites within feeding territories. Considering the limits of current knowledge, it would seem premature to give much weight to the display differences I observed.

One characteristic of the courtship of Lava Herons that stood out was its apparent perfunctory quality, lacking the intense aggressive behavior described for the Green-backed Heron by Meyerriecks (1960). Such a difference may reflect mutual recognition between potential Lava Heron mates. Failure of the female to respond to a potential supplanting attack, boldness of the female in entering the nest bush and periodically poking at the male, limited aggressive forward behavior by the male, early copulation attempts off the nest-site, and ease of final access of the female to the nest all may be explained by familiarity of the two birds with each other. The very limited development of color parts in the female compared to the male may also reflect a lessened need for a recognized female to be identified by the male as in breeding readiness in order to effect her entrance into his territory. Snow’s (1975) observations support my suggestion insofar as she found that the same birds may breed together in successive nesting episodes. Displays might be expected to be less complex when birds familiar with each other form pairs.

Thus, it appears then that most differences observed between Lava Herons and the Green-backed Herons studied by Meyerriecks (1960) reflect the former’s possession of a territory that is held throughout the year. Long-term occupancy leads to continued association and
recognition of neighboring birds. As noted by Snow (1975), repeated breeding through the year would be facilitated by repetition in mate choice, which could result in abbreviated courtship, comparatively rapid lowering of aggressive tendencies, and simplification and truncation of courtship displays.

Acknowledgments.—This study was supported in part by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and by the Charles Darwin Research Station. I thank B. Gutierrez-Guerrero and M. Spalding for assistance in the field and H. Hoek for his support throughout the study. I also thank D. Beaver, J. Barlow, T. Custer, D. Mock, and B. Snow for reviewing and making many useful suggestions on the manuscript. This report is a contribution from the Charles Darwin Research Station.—JAMES A. KUSHLAN, 19650 S. W. 264th Street, Homestead, Florida 33031. Accepted 15 June 1982.


Pre-migratory behavior of Common Loons on the autumn staging grounds.—Animals are frequently depicted as social or non-social organisms. Evidence indicates that such rigid categorizing should be reevaluated (Stacey and Bock, Science 202:1298–1300, 1978). Common Loons (Gavia immer) claim large territories as mated pairs during the summer breeding season and have developed a reputation as non-social birds. They are highly visible at this time, and because lakes smaller than 100 ha are rarely occupied by more than a single pair, loons are termed “solitary.”


Study site and methods.—Mille Lacs Lake is a large (54,000 ha) shallow lake in Aitkin, Crow Wing, and Mille Lacs counties in central Minnesota, and is known for its walleye (Stizostedion vitreum) sport fishing. The major fish species in terms of biomass is yellow perch (Perca flavescens), and cisco (Coregonus artedi) is sufficiently abundant to provide an annual commercial harvest.

Observations were made 2–3 days each week from 24 September–11 November 1975; we were at the site daily from 20–25 October. Aerial surveys were made on 6, 20, and 25 October, and 3 and 11 November. The entire lake was covered during the first four surveys. Only the west side was covered during the last flight and the survey discontinued because we found no loons.

Shore surveys were made periodically from all vantage points around the lake, principally on the west side after it was found to be the site of most loon concentrations. On 21 October we followed loon flocks by boat from 09:15–11:45 and from 17:00–20:00. On October 22 and 23 we made continual observations from 07:30–10:30 CDST with one observer at each of two locations. All shore and boat surveys were made with 40× spotting scopes and/or 10 × 50 binoculars.

Results.—(1) Lake use. Loons congregate primarily on the west and northwest sides of the lake. Mille Lacs has a gradual slope over much of the lake (3000–6000 m to the 7.5 m contour line) but in some places the slope is steeper (<1800 m to the 7.5 m line) and feeding groups
were usually located at those sites with steeper slopes. Islands on the southwest and southeast sides were other points of diurnal loon concentrations.

Loons were most numerous during the last week in October when their number peaked at 600–750 (Fig. 1). Aerial surveys are more accurate indicators of total numbers, but shore surveys were made more often, and data from them are also presented to confirm the trend shown from aerial surveys.

(2) Flying occurred primarily in the early morning when loons flew (75%) or swam in small groups from offshore rafting sites to inshore feeding locations from 08:00–08:45 (Fig. 2). Maintenance activity was predominant in late afternoon and no sleeping was seen at any time.

Feeding began about 09:00, declined from 11:00–12:00, and resumed after noon. Loons continued to forage all afternoon with a peak of activity between 14:00 and 16:00 when 85% of the birds were feeding. Most birds stopped by 17:15 and all birds ceased just prior to sundown.

Each feeding bout included the same sequence: peering by all group members, diving by one bird followed at once by diving by the rest, surfacing after 20–30 sec, and resumption of peering. Surface/underwater activities were coordinated and nearly simultaneous within feeding groups.

(3) Spatial relationships. Loons were recorded as singles or as group members, and the following figures are a composite from the 2 days in which we monitored all activities. From a total of 2218, 186 were lone birds and the rest were in flocks. Some lumping of group size
was necessary, e.g., 15–20, 30–35, because distance between observers and birds was great, and the diving of flock members made exact counts impossible in all instances; however, precise counts were secured for 70 of the 103 groups recorded.

Most groups contained fewer than 20 individuals (Fig. 3). A test for random distribution of group size showed it was clumped (\( \chi^2 = 17.47, \text{df} = 9, P < 0.05 \)), although the occasional formation of large groups gives a bimodal appearance to the histogram in Fig. 3. Feeding flock sizes were smaller than those with loons engaged in other activities; over 80% of all feeding groups had 20 or fewer individuals while only 47% of the other groups did.

Birds swam offshore in small groups at dusk. Rafting times were positively correlated with sunset times, later early in the fall and earliest in November. We followed six units of 10–30 birds (\( n = 21 \) birds/group) to their rafting sites by boat and found that although all birds rafted over the deepest part of the lake, the small groups remained as discrete units so that a single large aggregation did not occur. We surmised these groups remained intact overnight as we noted that birds also moved inshore in the morning as small units.

Discussion.—(1) Activity patterns. Feeding dominated afternoon activity (78.5% of all be-
Fig. 3. Number of loon groups in each size category. The line is the expected distribution if groups follow a Poisson distribution; bars are observed values presented as grouped data. Numbers below the histogram indicate upper limit of each column’s interval; numbers above each column are number of groups in each category. Upper histogram includes loons engaged in all activities; lower histogram includes only feeding groups.

behavior between 13:00 and 17:00). However, total daily foraging time (46.3%) was slightly less, but not significantly so, from time spent foraging on the wintering grounds (55.3%, McIntyre 1978), hence daily budgets allotted approximately equal time to feeding and non-feeding activities in both seasons. We had not expected this; rather we had anticipated that loons would spend more time feeding just prior to migration than when on the wintering grounds. This may indicate that they stop frequently during migration and do not require an abundance of migratory fat; or it may provide a clue that food is more abundant and/or readily available at Mille Laes Lake than it is in coastal waters in the winter, or it may suggest that energy requirements for loons are greater during the winter.

Location of rafts over maximum water depths as shown on lake contour maps, number of individuals in each, and time of day the birds settled were similar to rafting patterns on the wintering grounds (see McIntyre 1978 for techniques used to map loon locations). Loons are visual, diurnal predators (Barr, Ph.D. thesis, Guelph Univ., Guelph, Ontario, 1973) and the positive correlation between rafting and sunset times in both studies reinforces the concept that feeding time is related to light levels.

Rafting by groups as individual units assures “ready-made” feeding associations in the
morning. This practice may assure: (a) continuation of optimal foraging group size day after day; (b) that individuals known to each other will feed together daily, which may in turn result in feeding efficiency by reducing aggressive levels (Morse, Ecol. Monogr. 40:119–168, 1970); or (c) that rafts function as information centers to decrease search time to feeding sites (Siegfried, Trans. Roy. Soc. Afr. 39:419–443, 1971; Krebs, Behaviour 51:99–131, 1974). These are only speculations on our part, but are questions for future studies.

Loons raft offshore during all times of the year (McIntyre, Ph.D. thesis, Univ. Minn., Minneapolis, Minnesota, 1975; 1978; this study). The possibility that remaining offshore and in deep water promotes safety from potential predators and minimizes tidal effects has been offered as an adaptive value for winter rafting (McIntyre 1978). In the fall, lakes begin freezing along the shoreline and remain open longest over deep water. Loons may raft offshore in late fall to minimize chances of becoming trapped in ice should a lake begin to freeze during the night. It is very likely there are different primary selective pressures operating at different times of the year, and a single factor should not be invoked for all seasons.

(2) Social relationships. Selective pressures favoring social feeding include predator avoidance and increased foraging efficiency (Hamilton, J. Theoret. Biol. 31:295–311, 1971; Cody, Theoret. Pop. Biol. 2:142–158, 1971), assuming that they ultimately contribute to increased fitness. As we know of no loon predators at Mille Lacs Lake, we reason that the proximate selective factor in social feeding is related to maximizing foraging efficiency.

Feeding associations include 10–20 members in most instances. Larger groups arose through occasional convergence of smaller units (sudden concentrations of food?). The fact that loons stayed in small groups overnight lends credence to the idea that there are “basic” small groups (neighbors from the breeding grounds?); however, stability of these smaller units awaits testing using marked individuals.

This is the only time during the year when Common Loons are known to consistently feed in flocks. Animals do switch strategies in response to ecological conditions (e.g., Krebs 1974; Gill and Wolf, Ecology 56:333–345, 1975; Stacey and Bock 1978). We suggest that behavioral flexibility may be the usual mode for migrants whose resource base changes as a factor of location as well as for non-migrants subjected to seasonal resource variability. Long term studies of the annual biology of many species should be encouraged in order to answer more general questions of strategy-switching behavior.

Acknowledgments.—This study was conducted with the cooperation and logistic support of the Minnesota Department of Natural Resources, the U.S. Fish and Wildlife Service, and the Canadian Wildlife Service. J. Winship, J. Engelbrecht, and W. Johnson flew us on our aerial surveys; C. Burrows, R. Lorenz, J. Maloney, and J. Savada supplied information on Mille Lacs fishing populations; and M. Moore, J. Fellagy, H. Welty, P. Lang, and T. Savaloja provided information on former observations of loons on Mille Lacs. We thank them for their help. In particular we acknowledge the assistance of J. Bryant. We thank L. Wolf and R. Storer for comments on the manuscript, and T. Starmer and M. Petersen for help with the statistical analysis. K. Starczewski did the figures. Financial support came from the Oikos Research Foundation and NSF grant #8106567.—JUDITH W. MCINTYRE, Dept. Biology, Utica Coll., Syracuse Univ., Utica, New York 13502 and JACK F. BARR, 91 Forest St., Guelph, Ontario NIG 1J3 Canada. Accepted 5 July 1982.


Loon migrations off the coast of the northeastern United States.—In eastern North America the Common Loon (Gavia immer) breeds throughout boreal and arctic life zones, whereas the range of the Red-throated Loon (G. stellata) is farther north (82°N) but not as far south, reaching its southern limit in Newfoundland and the Gaspé Peninsula (Todd, Birds
L. Relative distribution and abundance of Common Loons in spring (April–June) off the northeastern United States. The number of loons divided by the number of standard bird counts (effort) per 10-min block of latitude and longitude is indicated.

Fig. 1. Relative distribution and abundance of Common Loons in spring (April–June) off the northeastern United States. The number of loons divided by the number of standard bird counts (effort) per 10-min block of latitude and longitude is indicated.

Fig. 2. Relative distribution and abundance of Red-throated Loons in spring (April–June) off the northeastern United States. The number of loons divided by the number of standard bird counts (effort) per 10-min block of latitude and longitude is indicated.

Mammals in the Northern Chesapeake Bight, U.S. Fish and Wildl. Serv., Biol. Serv. Program, FWS/OBS-80/04, 1980) is the first author to provide evidence of an offshore component. In this paper we examine differences in the temporal and spatial aspects of migrations of Common and Red-throated loons in coastal and offshore waters along the northeastern United States.

Methods.—Sightings of loons at sea were recorded by observers stationed on National Marine Fisheries Service (NMFS) and U.S. Coast Guard (USCG) vessels from 1977–1980 in a survey of the pelagic distribution of marine birds from Cape Hatteras (ca. 35°N) north to the Bay of Fundy (ca. 44°N) and from the coast seaward to 65°W. Observers made at least
Fig. 3. Relative distribution and abundance of Common Loons in autumn (September–November) off the northeastern United States. The number of loons divided by the number of standard bird counts (effort) per 10-min block of latitude and longitude is indicated.

one standard 10-min count (Brown et al., Atlas of Eastern Canadian Seabirds, Canadian Wildl. Serv., Ottawa, Canada, 1975) of all seabirds every 30 min while the ship was underway, noting the location, date, and local time at the start of each count. Number, behavior, and flight direction were recorded for all species seen during the counts. Similar data were collected for sightings of loons between standard counts. The number of standard counts was proportional to observation time between counts, and counts were made throughout daylight hours. Therefore, effort (number of standard counts) was used as an index of observation time. There were no sightings of loons from July–August and few from Decem-
Fig. 4. Relative distribution and abundance of Red-throated Loons in fall (September–November) off the northeastern United States. The number of loons divided by the number of standard bird counts (effort) per 10-min block of latitude and longitude is indicated.

Numbers of loons were recorded migrating south past a coastal promontory (10 m ASL), Manomet Point, Plymouth, Plymouth Co., Massachusetts (41°56'N, 70°33'W, Fig. 1) in autumn from 1972–1976 and in 1978. Two observers with binoculars and a 20× telescope counted migrants of all species over the sea, while principally censusing scoters (Melanitta spp.). We calculated a weekly rate of passage (loons/h) for 10 periods from 17 September–25 November by dividing the number of loons seen by hours of observation for each period.
### Table 1

**Breakdown of Observations of Offshore (No. 10-min counts) and Near-shore Sightings of Loons (h of Observation)**

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Month</td>
<td>No. 10-min counts</td>
</tr>
<tr>
<td></td>
<td>71°–76°W</td>
</tr>
<tr>
<td>Mar.</td>
<td>278</td>
</tr>
<tr>
<td>April</td>
<td>435</td>
</tr>
<tr>
<td>May</td>
<td>139</td>
</tr>
<tr>
<td>June</td>
<td>308</td>
</tr>
<tr>
<td>Sept.</td>
<td>186</td>
</tr>
<tr>
<td>Oct.</td>
<td>489</td>
</tr>
<tr>
<td>Nov.</td>
<td>141</td>
</tr>
<tr>
<td>Dec.</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results.—Figs. 1–4 show the offshore abundance of Common and Red-throated loons during spring and fall migration by 10-min blocks of latitude and longitude. The abundance of birds was calculated by dividing the numbers of loons observed in each 10-min block by the number of standard counts in that block.

In spring, 819 Common Loons were recorded from 460 sightings (1.8 loons per sighting). (A sighting is defined as an observation of an individual or distinct group of loons.) Another 160 loons in 81 sightings were unidentified. Common Loons were observed in offshore waters from 27 March–21 June, although 98% of the sightings were from April and May. Migration peaked in April southwest of Long Island and in May off the New England coast. Spring migrants occurred throughout waters of the continental shelf (Fig. 1). The majority of sightings were concentrated within 60 km of the coast south of Long Island, with one sighting noted 170 km east of New Jersey. East of Long Island distribution was more dispersed as Common Loons were seen up to 160 km to the south, east, and northeast of Cape Cod. A total of 49 Red-throated Loons was recorded from 31 sightings (1.6 loons per sighting), which represented 5% of the total number of spring loon sightings. Red-throated Loons were observed from 17 April–27 May. The distribution of Red-throated Loons in spring (Fig. 2) was similar to that of Common Loons (Fig. 1) as birds were observed throughout shelf waters.

In autumn, 212 Common Loons were recorded from 117 sightings at sea (1.8 loons per sighting). Another 51 loons in 27 sightings were unidentified. Common Loons were observed in offshore waters from 12 September–5 December and from 15 September–25 November (latest date of observer effort) at Manomet Point. Offshore migration was heaviest during November throughout the study area. The offshore distribution of Common Loons in autumn was similar to that of spring (Fig. 3), except that fewer birds were observed south of Long Island. The paucity of sightings off the mid-Atlantic states may be related to patchy effort west of 71°W during November (Table 1). We observed movement of Common Loons across the southern Gulf of Maine and northern Georges Bank in mid- to late November (Fig. 3), which was similar to that observed from late April to early May (Fig. 1). In contrast, autumn migration of Common Loons at Manomet Point peaked at 7.5 loons/h from 22–28 October,
and declined to 2.5 loons/h by 12–18 November. A total of 44 Red-throated Loons was recorded from 12 sightings (3.7 loons per sighting), which represented 8% of the total number of loon sightings in autumn. Red-throated Loons were observed in offshore waters from 22 October–1 December, and from 30 September–25 November (latest date of observer effort) at Manomet Point. The frequency of sightings peaked in November in both near-shore and offshore waters. The offshore distribution of Red-throated Loons in autumn (Fig. 4) was similar to that in spring (Fig. 2). In contrast to the offshore results, we found a substantial coastal migration of Red-throated Loons. An initial movement of 5.4 loons/h occurred from 22–28 October, but a greater and more extended peak of 7.4–7.8 loons/h passed Manomet Point from 3–18 November, which was equivalent or greater in magnitude than the Common Loon flight. By the week of 19–25 November activity dropped to 0.3 loons/h.

The behavior of loons in offshore waters for spring and autumn was divided into three categories: sitting, migrating (flying NW to NE in spring, SE to SW in fall), and flying (flying,
but not in the appropriate direction). Behavior was noted in 508 sightings of Common Loons; 111 were sitting, 366 were migrating, and 31 were flying. The frequency of sightings of migrating loons was greatest in early morning hours (05:00–08:00) and low throughout the rest of the day (Fig. 5). In spring, Williams (Wilson Bull. 85:230, 1973) rarely noted Common Loons migrating after 09:30 at a coastal location along the Gulf of Mexico. Kerlinger (Condor 84:97–100, 1982) observed Common Loons migrating from 2–9 h after sunrise in central New York state. The behavioral data for offshore sightings of Red-throated Loons were insufficient to reveal any conclusive pattern of daily timing. The near-shore data from Manomet Point were not analyzed, since observation effort was biased toward morning hours.

Discussion.—Our data show a substantial offshore migration of Common Loons in both spring and autumn, while Red-throated Loons occur with less frequency away from the coast. The proportions of Red-throated to Common loons at a coastal site in Massachusetts during autumn, when compared to their abundance offshore, indicate that substantial numbers of Red-throated Loons migrate near shore (cf. Ward, Records of New Jersey Birds 6:2–4, 1980). The offshore distribution of both species conforms to waters over the continental shelf (shoreward of the 200-m isobath); thus, sightings off the mid-Atlantic states are closer to shore and less dispersed than in waters northeast of Long Island (Figs. 1–4).

Forbush (1925) and Hill (1965) indicated that Common Loons principally migrate over Cape Cod, but another flight remains at sea outside of Cape Cod. Our offshore data confirm the latter flight since we found Common Loons passing south of the Cape Cod islands of Nantucket and Martha’s Vineyard. These loons probably cross the southern Gulf of Maine to or from Nova Scotia. The timing of this movement in autumn (mid-November), which differs from peak flights at Manomet Point (late October), suggests that different populations of Common Loons are using different migration routes. The offshore component may be breeders from Nova Scotia and Newfoundland, whereas the coastal movement may originate from the mainland of eastern Canada. Such an hypothesis may explain why there is no substantial migration of Red-throated Loons away from the coast, since their breeding range does not extend as far east along the Atlantic coast as that of Common Loons.

Acknowledgments.—We are indebted to the many volunteers from the Manomet Bird Observatory (MBO) who collected much of the data and to NMFS and USCG allowing observers aboard their vessels. J. M. Riccitelli compiled the coastal data from Manomet Point and E. H. Backus drew the figures. J. A. Hagar, N. P. Hill, and J. McNeasy provided helpful comments on an earlier version of this manuscript. This study was supported with funding from the U.S. Dept. Energy (DOE Contract No. DE-AC02-78EV04706), U.S. Fish and Wildlife Service (USFWS Contract No. 14-16-0005-6057) and private grants to MBO.—KEVIN D. POWERS AND JEFFREY CHERRY. Manomet Bird Observatory, Manomet, Massachusetts 02345. (Present address JC: Dept. Biological Sciences, State Univ. New York, Albany, New York 12222.) Accepted 25 Apr. 1982.

Table 1
RESPONSES OF TERRITORIAL MALES TO SONGS OF NEIGHBORING MALES AT TERRITORIAL BOUNDARY

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. &quot;chips&quot;</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>9.4</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0.5</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>10.1</td>
<td>1.9</td>
<td>6.1</td>
<td>0.4</td>
<td>0.7</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>10.2</td>
<td>1.7</td>
<td>5.0</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>PTP vs P</td>
<td>NS (^b)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>PTP vs PP</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P vs PP</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

\(^a\) Values for responses are averages for all tests; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, N = 5.

\(^b\) P < number given, NS = not significant.

However, there is often considerable intraspecific variation in bird song, and songs are frequently characteristic for each individual. This variation suggests the probability of individual recognition. Such recognition has been demonstrated for the White-throated Sparrow (Zonotrichia albicollis) (Brooks and Falls, Can. J. Zool. 53:879-888, 1975), Stripe-backed Wren (Campylorhynchus nuchalis) (Wiley and Wiley, Behaviour 41:10-34, 1976), and Common Yellowthroat (Geothlypis trichas) (Wunderle, Auk 95:389-395, 1978).

The songs of male and female Black-headed Grosbeaks (Pheucticus melanocephalus) exhibit considerable intraspecific variation (Ritchison, Ph.D. diss., Utah State Univ., Logan, Utah, 1980). Such variation probably provides ample information for individual recognition. The objective of this study was to determine if male and female Black-headed Grosbeaks can discriminate between the songs of neighboring and non-neighboring male and female conspecifics.

Materials and methods.—Fieldwork was conducted during the breeding season of 1978 at...

Table 2
RESPONSES OF TERRITORIAL MALES TO SONGS OF NON-NEIGHBORING MALES AT TERRITORIAL BOUNDARY

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. &quot;chips&quot;</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>9.30</td>
<td>0.90</td>
<td>4.00</td>
<td>0.40</td>
<td>0.20</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>3.30</td>
<td>22.10</td>
<td>6.70</td>
<td>2.60</td>
<td>5.20</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>8.40</td>
<td>8.00</td>
<td>8.70</td>
<td>0.10</td>
<td>0.80</td>
</tr>
<tr>
<td>PTP vs P</td>
<td>0.005(^b)</td>
<td>0.005</td>
<td>0.005</td>
<td>0.025</td>
<td>0.005</td>
</tr>
<tr>
<td>PTP vs PP</td>
<td>NS</td>
<td>0.005</td>
<td>0.01</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P vs PP</td>
<td>0.01</td>
<td>0.01</td>
<td>NS</td>
<td>0.01</td>
<td>0.025</td>
</tr>
</tbody>
</table>

\(^a\) Values and significance levels derived as in Table 1, N = 6.

\(^b\) P < number given, NS = not significant.
Malibu-Guinavah Campground in Cache National Forest, 10 km east of Logan, Cache Co., Utah. Experiments began on 24 May and continued until 8 July. Throughout this period playback experiments were conducted to determine if the birds could discriminate among songs of different individuals. All experimental birds were captured in mist nets and color banded to facilitate identification.

Birds with common territorial boundaries were referred to as neighbors and those from areas at least 8 km distant were designated strangers. Because birds were exposed to songs of neighboring males daily, it was assumed they had little or no previous contact with songs of strangers.

Each experiment consisted of three 5-min segments. During the first 5 min (pre-test period), undisturbed, ongoing behavior was observed. During the second 5 min (test period) songs were played every 15 sec, an interval characteristic of an undisturbed singing bout (Ritchison, pers. obs.). The final 5 min (post-test period) was used again for observation. Throughout each test all sounds and non-vocal behavior were noted.

### Table 3

**Responses of Territorial Males to Songs of Neighboring Males Within Territory**

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. “chips”</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>5.30</td>
<td>1.60</td>
<td>9.00</td>
<td>0</td>
<td>1.40</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>4.70</td>
<td>10.10</td>
<td>11.90</td>
<td>0.40</td>
<td>4.60</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>6.70</td>
<td>4.60</td>
<td>11.30</td>
<td>0</td>
<td>1.00</td>
</tr>
<tr>
<td>PTP vs P</td>
<td>NSb</td>
<td>0.005</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>PTP vs PP</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P vs PP</td>
<td>0.01</td>
<td>0.01</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Values and significance levels derived as in Table 1, N = 5.

b $P <$ number given, NS = not significant.

### Table 4

**Responses of Territorial Males to Songs of Non-neighboring Males Within Territory**

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. “chips”</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>6.90</td>
<td>4.20</td>
<td>6.40</td>
<td>0.70</td>
<td>0.60</td>
</tr>
<tr>
<td>Test period (P)</td>
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<td>27.30</td>
<td>7.70</td>
<td>2.20</td>
<td>6.20</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>5.80</td>
<td>16.60</td>
<td>10.10</td>
<td>0.10</td>
<td>2.80</td>
</tr>
<tr>
<td>PTP vs P</td>
<td>0.005b</td>
<td>0.005</td>
<td>0.005</td>
<td>0.025</td>
<td>0.005</td>
</tr>
<tr>
<td>PTP vs PP</td>
<td>NS</td>
<td>0.005</td>
<td>0.005</td>
<td>NS</td>
<td>0.005</td>
</tr>
<tr>
<td>P vs PP</td>
<td>0.005</td>
<td>0.005</td>
<td>NS</td>
<td>0.01</td>
<td>0.01</td>
</tr>
</tbody>
</table>

* Values and significance levels derived as in Table 1, N = 6.

b $P <$ number given, NS = not significant.
Table 5
Comparison of Responses of Territorial Males to Playback of Songs of Neighboring and Non-neighboring Males at Territorial Boundary*

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. &quot;chips&quot;</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>NS (^b)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>0.01</td>
<td>0.005</td>
<td>0.005</td>
<td>NS</td>
<td>0.025</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>0.01</td>
<td>0.005</td>
<td>0.01</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Values compared are listed in Tables 1 and 2, respectively; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed. N = 3.

\(^b\) \(P < \) number given, NS = not significant.

Each bird was tested twice with each of the following: (1) the mate's song; (2) the neighboring male's song; (3) the songs of non-neighboring males; and (4) the songs of non-neighboring females. Different trials with the same bird, using either male or female song, occurred at least 2 days apart, i.e., tests with the songs of males were at least 2 days apart; however, tests with the songs of one sex were conducted 1 day before or after tests with the songs of the other sex. The sequence of test songs played to each bird and the order in which birds were tested each day were random. All experiments were conducted between 05:00 and 11:00 MDT.

Speaker locations for the respective tests were: (1) at the approximate center of the territory for songs of mates and strange females and (2) at both the territorial boundary and at the center of the territory for songs of neighboring and non-neighboring males. At the boundaries the speaker was directed toward the center of the territory to minimize the neighbor's responses. At the center, speaker orientation was not standardized. Boundaries were established for each territory by observation of encounters and by preliminary experiments using playback of the songs of non-neighbors (different from those used later).

Recordings were made using an Altec 633A microphone mounted in a 62-cm parabolic reflector with a Nagra IIIB recorder at a tape speed of 19 cm per sec (71/2 ips). Experimental tapes were prepared using previously recorded songs of mates, neighbors, and non-neigh-

Table 6
Comparison of Responses of Territorial Males to Playback of Songs of Neighboring and Non-neighboring Males Within Territory*

<table>
<thead>
<tr>
<th></th>
<th>Closest approach (m)</th>
<th>No. songs</th>
<th>Syllables per song</th>
<th>No. &quot;chips&quot;</th>
<th>No. flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>NS (^b)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>0.005</td>
<td>0.005</td>
<td>0.005</td>
<td>0.005</td>
<td>0.01</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>0.01</td>
<td>0.005</td>
<td>0.01</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Values compared are listed in Tables 3 and 4, respectively; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed. N = 5.

\(^b\) \(P < \) number given, NS = not significant.
Table 7

Responses of Incubating/Brooding Females to Songs of their Mates*

<table>
<thead>
<tr>
<th></th>
<th>No. songs</th>
<th>No. &quot;chips&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-test period (PTP)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Test period (P)</td>
<td>0</td>
<td>6.80</td>
</tr>
<tr>
<td>Post-test period (PP)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PTP vs P</td>
<td>—b</td>
<td>0.005</td>
</tr>
<tr>
<td>PTP vs PP</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P vs PP</td>
<td>—</td>
<td>0.005</td>
</tr>
</tbody>
</table>

*Values for responses are averages of all tests; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, N = 6.

b P < number given.

Borders. Each tape was 5 min in duration with songs spaced at 15-sec intervals. For playback a portable speaker was connected to an amplifier and the Nagra and placed in a bush or small tree 2–3 m above ground.

Criteria of response.—To obtain a quantitative measure of a bird’s reaction to playback the following features of response were used. (1) Number of songs and syllables per song. Grosbeak songs vary considerably in the number of syllables per song and observations indicated a relationship between the number per song and a bird’s level of excitement (Ritchison, pers. obs.). Therefore, the number of syllables in each song was counted as well as the total number of songs uttered by the experimental bird. Syllables were uttered by the grosbeaks at a rate that allowed me to count them individually. (2) Latency to the first song. The time from the beginning of the experiment (the start of the test tape song) to the time when the experimental bird first sang was noted. (3) Distance of closest approach. The distance of the experimental bird’s closest approach to the speaker during the playback was noted. (4) Number of flights. Short flights (i.e., less than 50 cm) and non-flight movements were not counted. If it was obvious from the relative location of consecutive vocalizations that the bird had made an unobserved flight, this movement was counted. Since some flights were missed, this number was a minimum value. (5) Number of “chips.” Grosbeaks gave these calls in a number of situations. At times these calls appeared to indicate anxiety or distress and at other times they appeared to function as location calls between mates. The total number of these vocalizations given during each 5-min segment of the experiment was counted.

The above measures were compared for the same birds responding to different songs at the same locations and to the same songs in different locations. The Wilcoxon matched-pairs signed-ranks test was used for all statistical comparisons (Siegel. Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York, New York, 1956).

Results.—Males responded to the songs of non-neighbors in a significantly different fashion than they did to the songs of neighbors at both the territorial boundary and the center of the territory (Tables 1–6). This was true for all measures of response during playback (with the exception of number of flights at the center of the territory). In the post-playback period at the boundary, there were significant differences in response for three of the five categories of response and, at the center of the territory, in one of the five categories (number of songs). Thus, it is clear that neighbor/non-neighbor discrimination by song occurred at the boundary and at the center of the territory.
Differences in male response to the same type of song given at the different locations are less clear. Comparisons of responses to the songs of non-neighbors at the territorial boundary and at the center of the territory revealed but one significant difference ($P < 0.01$): playback of the songs of non-neighbors at the center of the territory elicited more singing in the post-playback period. In general, however, responses to the songs of non-neighbors at the territorial boundary and at the center of the territory were similar.

Two measures of response (approach distance and numbers of songs) revealed significantly different reactions ($P < 0.025$) by males to the songs of neighbors at the center of the territory than at the territorial boundary. Females showed no responses to the songs of either neighboring or non-neighboring males. They did, however, respond significantly to the songs of their mates (Table 7). Neither males nor females responded to the songs of non-neighboring females. In addition, territorial males showed no significant responses to the songs of their mates ($P > 0.025$).

**Discussion.**—The results of the playback experiments indicate that territorial male Black-headed Grosbeaks responded with different intensity to the songs of different males of their own species. More precisely, they distinguish between familiar songs of neighbors and unfamiliar songs of non-neighbors.

Discrimination between the songs of neighbors and non-neighbors was achieved very quickly. Latency to the first song generally was less when a strange song was played, and at times only one rendition of the song was necessary to elicit singing by the test bird.

Weeden and Falls (Auk 76:343–351, 1959), Goldman (Auk 90:106–113, 1973), and Brooks and Falls (1975) found that Ovenbirds (Seiurus aurocapillus), Field Sparrows (Spizella pusilla), and White-throated Sparrows, respectively, could distinguish between songs of neighbors and non-neighbors and that in these species the reactions to the songs of non-neighbors were stronger. In each of these species, as well as in the Black-headed Grosbeak (Ritchison 1980), each individual possesses a distinctive song (or syllable repertoire) which remains more or less constant throughout the breeding cycle. Therefore, males of these species have ample opportunity to learn the distinctive songs of their neighbors. Presumably, such learning accounts for the differential strength of response to songs of neighbors and non-neighbors.

Evidence suggests that decreased response to a neighbor’s songs results from habituation. For example, Falls (1963) found that Black-backed Magpies (Gymnornphina tibicen) habituated to playback of recorded songs as well as to the location from which they were broadcast. Petrovich and Peeke (Behav. Biol. 8:743–748, 1973) reported habituation in the response of White-crowned Sparrows (Zonotrichia leucophrys) to playback and found that response decrement was specific to the particular song played.

What is the function of such habituation? Reduced responses to neighbors, which do not pose as great a threat as do strangers to the integrity of the territory, may diminish risks and save energy for other activities (Brooks and Falls 1975). Further, any behavior which increases the probability of a male’s detecting significant changes from the status quo should have survival value. Ability to recognize the songs of each neighbor would allow the detection of new birds and/or the displacement of existing neighbors, situations that could easily pose a threat to a bird’s territory. The importance of detecting such changes becomes apparent upon examination of the results of removal experiments reported by Brooks and Falls (1975).

In contrast to the responses shown by territorial males to the songs of other males, they showed no response to the playback of songs of strange females. In other words, singing by female Black-headed Grosbeaks appears to have no territorial function. Other species have been reported in which the females’ songs apparently have no territorial function, e.g., Bullfinches (Pyrrhula pyrrhula) (Nicolai, Z. Tierpsychol. 13:93–132, 1956) and Northern Orioles (Icterus galbula) (Pugsley, News from Bird Banders 21:32–36, 1946). Armstrong (A Study of Bird Song, Oxford Univ. Press, London, England, 1963) divided passerine species
into two broad groups: (1) species in which the female sings and defends territory with the male and (2) species in which the female sings as well, or nearly as well, as the male, but the singing is concerned with pair-bond and/or family-group maintenance and not with the defense of territory. The results of the present study indicate that Black-headed Grosbeaks are another “group 2” species, since the singing of females has no territorial function. Previous studies indicate that such singing is important in the maintenance of the pair bond and of the family-group after fledging (Ritchison 1980).

Although females failed to respond to the songs of either neighboring or non-neighboring males, they did show a response when the songs of their mates were played back. Such a response indicates that female Black-headed Grosbeaks are able to recognize the songs of their mate. There have been several reports of such mate recognition in colonial seabirds (White, Anim. Behav. 19:125–131, 1971; Wooller, Z. Tierpsychol. 48:68–86, 1978; and others). However, mate recognition has rarely been documented in passerines.

Acknowledgments.—I am grateful to Keith Dixon for his help in all phases of this study. I also wish to thank E. C. Oaks, B. Gilbert, J. Gessaman, and I. Palmblad for their many helpful suggestions. J. Bruce Falls and M. Ross Lein made many helpful comments on the manuscript. This study was supported by grants from The Frank M. Chapman Fund of the American Museum of Natural History and from Sigma Xi.—GARY RITCHISON, Dept. Biology, Utah State Univ., Logan, Utah 84322. (Present address: Dept. Biological Sciences, Eastern Kentucky Univ., Richmond, Kentucky 40475.) Accepted 1 May 1982.


Vocal learning in the Parulinae.—Vocal learning is the ability to use auditory information, including feedback, to modify or enhance vocal development (Nottebohm, Am. Nat. 106:116–140, 1972). This learning is well documented in both humans and birds (e.g., Marler, Am. Sci. 58:669–673, 1970), and suspected in cetaceans (e.g., Payne and Payne, Z. Tierpsychol., in press) and perhaps non-human primates (Green, Z. Tierpsychol. 38:304–314, 1975). Among birds, evidence for vocal learning now exists for over 300 bird species (Kroodsma and Baylis, in Acoustic Communication in Birds, Kroodsma and Miller, eds., Academic Press, New York, New York, in press) from the Psittaciformes, Apodiformes, Passeriformes, and perhaps even the Piciformes (Wagner, Wilson Bull. 56:65–76, 1944) and the Galliformes (Sparring, Wilson Bull. 91:618–621, 1979).

Most documented examples of avian vocal learning are from the oscines, however, and in this group the Parulinae (wood warblers) is one of the largest subfamilies for which solid evidence of vocal learning is still lacking. Evidence from micro-geographical variation suggests that some song types among warblers are learned (Kroodsma, Auk 98:743–751, 1981). Herein we verify through both experiment and observation that males of the Common Yellowthroat (Geothlypis trichas) and Chestnut-sided Warbler (Dendroica pensylvanica) are capable of vocal learning.

One male Chestnut-sided Warbler nestling at about 10 days of age was taken into the laboratory and then tutored from day 25 to day 100 with a Common Yellowthroat witchity song type (see Fig. 1A) and nine different song types of Yellow Warblers (Dendroica petechia). Yellow and Chestnut-sided warbler songs are rather similar and often confused by field biologists; hence, it was reasoned that, if Chestnut-sided Warblers do develop songs through imitation, then Yellow Warbler songs would be likely hetero-specific songs that would be learned. The Common Yellowthroat song was used both to tutor a male Common Yellowthroat in an adjacent cage and as an additional song model for the Chestnut-sided
Vocal learning by the Common Yellowthroat and the Chestnut-sided Warbler. A. Common Yellowthroat tutor song, the typical *witchity-witchity* of wild males. B. Three songs of a laboratory-reared Chestnut-sided Warbler which was exposed to both Yellow Warbler songs and the yellowthroat song in A. Arrows indicate clear imitations of the yellowthroat tutor song. C. On the left is a typical Chestnut-sided Warbler “accented ending type 2” *chee* variant (see Lein 1978), with song components labelled a, b, c, and d. On the right is a song of a Common Yellowthroat from Charlton City, Massachusetts. Homologous song components are labelled, and this Common Yellowthroat typically concluded his song with several renditions of the typical conspecific *witchity* (only one of which is illustrated). These spectrograms are ink tracings of sonagrams made on a Kay 7029A Sona-Graph with a 300 Hz filter (ordinate is kHz, abscissa time).

This experimental Chestnut-sided Warbler was maintained on natural daylengths and then recorded as it came into song the next spring.

This Chestnut-sided Warbler developed four stable song types, three of which contained unmistakable elements of the Common Yellowthroat song type (Fig. 1B). In spite of the apparent similarity of the Yellow and Chestnut-sided warbler songs to the human ear, none of the Yellow Warbler songs or song elements were imitated. By default, all songs would be classified as “Unaccented,” for at no time did this male sing any typical “Accented Ending” (Fig. 1C; see also Figs. 1–3 in Lein, Can. J. Zool. 56:1266–1283, 1978).

Interspecific vocal learning was also documented in the Common Yellowthroat, but this time in the field. Meservey discovered near Charlton Center, Massachusetts, a male Yellowthroat singing both a typical Common Yellowthroat *witchity* song and an excellent copy of the “Accented Ending Type 2,” *chee* variant of the Chestnut-sided Warbler (Fig. 1C; see also Fig. 2 in Lein 1978). This male typically sang the Chestnut-sided Warbler song first, followed immediately by two to four repetitions of the conspecific song syllable. This particular song type of the Chestnut-sided Warbler varies little throughout the geographical range of the species, but some individuals do omit or deemphasize song component “b” in their
song types (e.g., Fig. 2D in Lein 1978 and Fig. 4B in Kroodsma 1981), just as this male
Common Yellowthroat did. Other than the slightly modified "c" note (song component c' in
Fig. 1C), this is a perfect copy of a Chestnut-sided Warbler Accented Ending song type.

Other suggestive evidence of vocal learning as a normal process in the Common Yellow-
throat comes from song development in the nestling male which was tutored simultaneously
with the experimental Chestnut-sided Warbler male discussed above. This male developed
a highly abnormal, simple song syllable, which was repeated in typical Common Yellowthroat
fashion. The repeated song component consisted of a single note, however, not the typical
three to six note syllable of wild birds (Borror, Living Bird 6:141-161, 1967). Such simplifi-
cation of song syllables typically occurs in isolated birds where conditions for vocal learning
are not sufficient for the normal complex song of the species to develop (e.g., Kroodsma.

Other than the micro-geographical variation of Unaccented Ending songs (or Type II songs)
in the Chestnut-sided Warbler and the Blue-winged Warbler (Vermivora pinus) (Kroodsma
1981), the only other possible evidence of vocal imitation in the Parulinae had involved
disputed examples of interspecific mimicry by the Yellow-breasted Chat (Icteria virens) (Grin-
U.S. Natl. Mus. Bull. 203, 1953). The evidence in our report is unequivocal, however, and
confirms the presence of vocal learning in the Parulinae. Such vocal learning among species
where different song types are used in different contexts raises interesting questions not only
about what males learn to sing but also about how they come to use these learned signals
in an intriguing vocal communication system.

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(BNS 78-02753 and BNS 80-40282).—DONALD E. KROODSMA, Dept. Zoology, Univ. Massa-
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City, Massachusetts 01508; AND ROBERTA PICKERT, Rockefeller Univ. Field Research Center,

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Factors affecting the performance of flight songs and perch songs in the Com-
mon Yellowthroat.—Flight songs have been reported for 11 species of wood warblers
(Parulinae) (Ficken and Ficken, Living Bird 1:103-121, 1962; Meanley, Wilson Bull. 80:72-
77, 1968), including the Common Yellowthroat (Geothlypis trichas). The flight songs are given
as the singer ascends to 10 m above the ground in slow, bobbing flight. The ascent is
accompanied by a series of sputtering notes ending with a portion of the perch song; the
1937) presents data showing that most flight-singing by the Ovenbird (Seiurus aurocapillus)
occurs late in the day and late in the season, and other workers have described a similar
tendency in yellowthroats (Bent 1953; Stewart, Wilson Bull. 65:99-115, 1953; Hoflund,
Proc. Minnesota Acad. Sci. 27:144-174, 1959). In this paper I examine factors influencing
the relative frequencies of yellowthroat flight song and perch song, and suggest a possible
function for the flight song in this species.

Yellowthroat singing behavior was studied on two oldfield study areas located in northern
In 1970 these areas supported seven yellowthroat territories and in 1971, six territories. In 1970
temperature and wind velocity 1 m above the ground were measured during observation
periods, and all songs were counted. Notes on behavior were taken during both field seasons.

Data from 1970 yielded 92 hour-long periods during which songs were counted. Multiple
regression analysis was used to examine the relative effects of four independent variables (temperature, time of day, wind velocity, and time of year) on the performance of flight and perch songs. Behavioral data from 1970 and 1971 were used to examine the effect of apparent motivational state on singing behavior. The numbers of perch-song and flight-song bout initiations were counted, and the birds were assessed as "undisturbed" or "disturbed" at the time of bout initiation. The term bout as used here refers to a series of songs, with the elapsed time between songs being less than 2 min. A silent period of more than 2 min was considered to mark the end of a bout. A bird was regarded as undisturbed if during the observation period it: (1) experienced no displaying or singing by any neighboring males, and (2) had not engaged in any territorial encounters during the preceding 5 min. A disturbed bird was one which did not meet these constraints. Of a total of 3139 min of observation, 1645 min were spent watching undisturbed birds and 1494 min were spent watching disturbed birds. Expected frequencies used in a Chi-square test for goodness-of-fit were based on the proportion of time birds of the two classes were under observation and the frequencies with which they began to sing one song type or the other. The breeding status of the birds was unknown.

During June of 1977 I recorded flight songs from a population of yellowthroats in eastern Monroe Co., Indiana. In only two instances was I able to record both the perch song and flight song from the same individual. The two pairs of sonograms from these birds showed that the portion of perch song incorporated in the flight-song performance was of the same phrase type (sensu Borror, Living Bird 6:141–161, 1967) as was used in that individual's perch-song performance.

Table 1 presents the results of the regression analysis of the 1970 song counts. Temperature, time of day, wind velocity, and time of year together explain 19.8% and 34.8% of the variation in the perch-song and flight-song count data, respectively. Of these four variables, only time of day and time of year had a significant effect on perch-song and flight-song performance. In general, perch-song performance decreased later in the day and later in the season. Flight-song performance increased with time of day and time of year, with the time of year being by far the more important variable.
The apparent motivational state of a bird was strongly related to the number of perch songs given. Undisturbed birds were seen to initiate 58 perch-song bouts, while disturbed birds initiated 114 perch-song bouts ($\chi^2 = 24.08, df = 1, P < 0.001$). Initiation of flight-song bouts was not significantly different between undisturbed and disturbed birds.

The relationship of flight song frequency to time of year is interesting, especially in light of the fact that the reproductive stage of the singers was unknown. Territorial boundaries were well defined early in the season, and after the first week of May in both field seasons intense territorial encounters became uncommon. This decline in territorial disputes may have been the result of resident males having established territorial boundaries and learned the songs of their immediate neighbors (Wunderle. Auk 95:389–395, 1978). The analysis of the yellowthroat flight-song recordings showed that the perch-song portion incorporated in the flight-song vocalization is characteristic of the individual, making individual recognition on the basis of the flight song performance possible. Song without visible displays has been shown to be sufficient to maintain territorial boundaries (Peek, Anim. Behav. 20:112–118, 1972; Krebs, New Scient. 70:534–536, 1976), and the increased visibility of a yellowthroat in flight would further enhance the deterrent effect of the vocalization. I therefore suggest that the yellowthroat flight song functions to maintain territorial boundaries, once these boundaries have been established. The relative infrequency of flight songs at all times during the season (Stewart 1953) may reflect the fact that this vocalization serves primarily to discourage trespassing by other males, unlike the perch song, which is used during the initial setting up of territories and territorial disputes, as well as for advertising for, and maintaining a pair bond with females (Wunderle 1978).

Acknowledgments.—I wish to thank Donald Kroodsma, Jon Barlow, Chris Oswald, and Craig Stewart for their helpful comments and suggestions. I am especially indebted to Val Nolan, Jr., who first inspired my interest in warbler behavior, and to whom this note is dedicated.—Michael P. Kowalski, 5690 Kings Rd., Bloomington, Indiana 47401. Accepted 1 Oct. 1982.


Vocalizations and behavior of Violet-green Swallows in the Chiricahua Mountains, Arizona.—The Violet-green Swallow (Tachycineta thalassina) has been largely ignored by ornithologists. The only published accounts of its basic biology date from the 1940s (Bent, U.S. Natl. Mus. Bull. 179, 1942; Edson, Auk 60:396–403, 1943) or must be gleaned from generalized state bird-books (e.g., Bailey, Birds of New Mexico, New Mexico Dept. Game Fish., 1928; Phillips et al., The Birds of Arizona, Univ. Arizona Press, Tucson, Arizona, 1964). Virtually nothing has been reported about its vocalizations.

In May–July 1980 I studied Violet-green Swallows and recorded their vocalizations in the Chiricahua Mountains, Cochise County, Arizona. Recordings were made with Uher 4000 Report I and 4000 Report 1C tape recorders and Uher M517 and Electrovoice Soundspot microphones, the former mounted in a 60-cm parabolic reflector. Tape speeds were 19 and 9.5 cps. Sonagrams were made on a Kay Elemetrics Corp. Sona-Graph Model 6061-B using wide-band pass setting and linear scale. All observations and recordings were made near Rustler Park (elev. 2545 m) and at the Southwestern Research Station (elev. 1636 m). I tape-recorded approximately 35 different individual swallows.

Violet-green Swallow vocalizations can be grouped into two broad classes, chee-chee and “twitter” calls.

Chee-chee calls.—These calls are generally mono- or disyllabic (syllable defined as a con-
Fig. 1. Sonagrams of Violet-green Swallow vocalizations from the Chiricahua Mountains, Arizona: A. *chee-chee* calls of adults, first three tracings from one bird, latter four each from different birds; B. *chee-chee* calls from three different juveniles, first two tracings from one bird, middle two from a second bird, latter three from a third; C. representative "twitter" calls, all from one individual.
tinuous tracing on a sonagram), range from about 2.5 to over 7 kHz, last about 165 msec, and occur in pairs or series (up to 4 sec in duration) with intervals of 85–165 msec between calls (Fig. 1A–B).

These vocalizations were used in several behavioral contexts, but almost invariably when one bird was associating with at least one other swallow. Many were recorded from foraging swallows. Violet-green Swallows regularly foraged on emerging crepuscular insects over the grounds of the Southwestern Research Station in late afternoon with White-throated Swifts (Aeronautes saxatalis) and bats (Myotis spp.). The calls were often given when two birds passed near each other in flight, or during intra- and interspecific chases. Violet-greens frequently chased each other during these foraging bouts, and on two occasions swallows chased bats. During June and July, Violet-green Swallows appeared at the research station only in the late afternoon, apparently being confined to coniferous forest at higher elevations at other times. Adult violet-greens also gave chee-chee calls when traveling to and from nesting sites at higher elevations. Occasionally chee-chee calls were mixed with “twitter” calls (see below). In flocks chee-chee calls possibly serve to promote social cohesion (“contact” calls), especially if these birds forage socially as suggested for Bank Swallows (Riparia riparia) (Emlen and Demong, Science 188:1029–1031, 1975).

I also recorded chee-chee calls (Fig. 1B) from perched juveniles of at least five broods assembled (at different times) in a large Arizona sycamore (Platanus wrightii) on the grounds of the research station. These juveniles apparently were still dependent on their parents for food. None was seen catching insects itself, and adults dropped insects into the juveniles’ mouths while hovering above them, as described for Purple Martins (Progne subis) (Brown, Wilson Bull. 90:376–385, 1978). The juveniles generally perched on an exposed branch, calling repeatedly, especially whenever another swallow flew near. The juveniles and their parents left at nightfall and returned at daybreak, suggesting that this tree was a “grouping area” (Brown 1978). These juveniles had probably been out of the nest at least 2–3 days when I recorded their vocalizations. They had to be old enough to travel a considerable distance, because I found no violet-green nest within 1 km.

Although the birds were unmarked, apparent nonparental swallows harassed these juveniles, and were chased away by parents. This behavior was similar to raider behavior described for Purple Martins (Brown and Bitterbaum, Wilson Bull. 92:452–457, 1980). Independent juvenile Violet-green Swallows (known by their more squarish tails) seemed attracted by the activity of the parents and the broods in the sycamore and acted as raiders. They gave chee-chee calls when chased away by parental swallows, and as they foraged and passed near other flying birds.

Chee-chee calls may also serve as contact calls between parents and offspring. When juveniles sat in dense foliage, parents probably could locate them only by sound. If parent–offspring recognition occurs in Violet-green Swallows, it may involve auditory recognition, as suggested by Beecher et al. (Anim. Behav. 29:95–101, 1981) for Bank Swallows.

“Twitter” calls.—These calls are generally monosyllabic (Fig. 1C). They range from 2–ca. 6.5 kHz. Some syllables have a duration as long as 125 msec and are longer than syllables of chee-chee calls. I detected no recognizable, repeating series of syllables which could be interpreted as a song.

“Twitter” calls apparently were restricted to interactions associated with courtship and territory establishment. They were recorded from recently arrived birds at Rustler Park near nesting sites. The calls were given only in flight as swallows flew to and from dead snags, investigating woodpecker holes. Some birds appeared to be paired and presumably the male was escorting the female to and from the site. Some individuals tried to establish ownership of certain holes, but interference from other swallows and Acorn Woodpeckers (Melanerpes formicivorus) prevented this. The Violet-green Swallows made low swoops, uttering a guttural
alarm call, at Acorn Woodpeckers in the snags. I was unable to record this alarm call, but it sounded similar to the *zwrack* alarm call of the Purple Martin (Johnston and Hardy, Wilson Bull. 74:243–262, 1962; Brown, pers. obs.). “Twitter” calls accompanied intraspecific fights, which consisted of short chases from the snags. I detected no obvious differences between sonograms of “twitter” calls used when escorting mates and those used when chasing intra-specific competitors.

At active nesting sites where violet-green pairs had established territories (and later as they built nests and incubated), “twitter” calls were never recorded. In such circumstances, the only vocalizations I recorded were occasional *chee-chee* calls as members of the pair circled nearby or flew away together. Once established at a site the swallows were largely nonvocal. Active nests were not studied during feeding of the young, so I do not know if the parents or young vocalized at that time.

Violet-green Swallows in the Chiricahua Mountains, although decidedly gregarious at times, were solitary nesters. Flocks of up to 40 birds foraged together at the research station, and groups of 10 commonly investigated unused nesting sites at Rustler Park or foraged together high in the mountains. But of the three active nesting sites I located in the Chiricahua, all contained single pairs only. Other holes were present in the snags containing active nests but were unused or defended by Acorn Woodpeckers that nested in adjacent snags. The situation in the Chiricahua is markedly different from the 20 pairs of violet-greens nesting as a colony near Santa Fe, New Mexico (Bailey 1928) or Bent’s (1942) reports of 20 pairs in a “single dead pine” in Colorado, colonies of up to 100 or more pairs in cliffs in Washington, and colonies of from 6–50 birds in Alaska. Thus, it seems that the Violet-green Swallow is highly colonial yet may also be a solitary nester. (However, to my knowledge there have been no reliable reports of large colonies in the last 40 years.)

Little has been published on vocalizations of other North American swallows, so it is difficult to compare violet-green vocalizations with those of other species (but see Samuel, Auk 88:839–855, 1971). With only two kinds of calls, however, it is possible that Violet-green Swallows do not rely heavily on vocal communication. If violet-greens are colonial through most of their range, this may have shaped the evolution of the vocal repertoire. As suggested by Marler (Behaviour 11:13–39, 1957), Wiley (Anim. Behav. 24:570–584, 1976), and Smith (The Behavior of Communicating, Harvard Univ. Press, Cambridge, Massachusetts, 1977), vocal communication in particular may be inefficient in colonies of birds because too many signals from different individuals impinge on the receiver at any given time, creating confusion (the “cocktail party effect”). Directional visual displays, which can be oriented to specific individuals, may be favored in colonial birds. Violet-green Swallows possess visual displays such as white flank patches that can cover the rump, and these birds may emphasize vocal displays only when moving flocks or concealed offspring cannot maintain visual contact.

Acknowledgments.—I thank the Austin College Biology Department for technical and financial assistance, and this paper constitutes part of a senior honors thesis approved by the Biology Department. The Southwestern Research Station of the American Museum of Natural History provided logistical support. W. Piper helped me in the field, and C. Erickson and W. Randall made my stay in Arizona enjoyable in many ways. M. L. Bomberger assisted with the figure. Finally, I thank Howard McCarley, my undergraduate advisor, and R. and K. Brown, my parents, for much assistance and encouragement.—CHARLES R. BROWN, Dept. Biology, Princeton Univ., Princeton, New Jersey 08544. Accepted 28 June 1982.
Female Tree Swallow lays three clutches during one breeding season.—The Tree Swallow (Iridoprocne bicolor) usually lays a second clutch only in response to the disturbance or failure of the first (Kuerzi, Proc. Linn. Soc. N.Y. 52–53:1–52, 1941; Bent, U.S. Natl. Mus. Bull. 179, 1942; Chapman, Bird Banding 26:45–70, 1955). Wedemeyer (Bird Lore 36:100–105, 1934), however, reported that Tree Swallows in his study area in Montana sometimes raised two broods. No instance of a female laying three clutches in one breeding season has been recorded previously.

For the past two years (1980, 1981) I have been conducting a study of the social behavior of the Tree Swallow in a salt marsh on the south shore of Long Island, New York (see Schaeffer, EBBA News 34:216–222, 1972, for a description of the area).

On 18 May 1981, I banded an adult Tree Swallow (U.S.F.W.S. aluminum band 960-27903) caught in Box 13 of my nest-box trail. At this time there were four eggs in the nest. I recaptured this bird in the same box on 19 May (five eggs) and on 21 May (six eggs). Behavioral observations indicated that this bird was a female although she was not seen incubating the eggs in Box 13 and no brood patch was apparent. After 21 May, this female and her probable mate were seen flying back and forth between Box 13 and Box 23 (40 m away), frequently perching on and entering Box 23. The female and her male abandoned Box 13 on 25 May. The next census of Box 13 on 13 July showed that the only remaining egg contained a partially developed embryo.

On 30 May, one egg was discovered in Box 23 even though the nest cup was not lined with feathers as is usual in Tree Swallows. On 31 May two eggs were in the nest and the box was defended by female 27903 and another bird. On 1 June there were two eggs (? 27903 was captured in the box) and on 2 June, three eggs were discovered. The female was never seen incubating and the three eggs were cold on 5 June. The disappearance of all three eggs prior to the next census on 13 July precluded the determination of their fertility.

On 10 June two eggs were discovered in Box 16. 125 m from Box 23. Box 16 contained a nest completed and lined with feathers then abandoned by a pair of swallows in the middle of May. Female 27903 was captured in Box 16 while incubating five eggs on 15 June. She successfully hatched all five eggs (26 June) and fledged all five nestlings (18 July). It is not known if female 27903 retained the same mate for each clutch. The Tree Swallow has been shown to have the ability to lay two and possibly three fertile clutches in one breeding season.

This research was funded by a Rutgers University Busch Memorial Grant to H. W. Power. I thank H. W. Power and E. Litovich for their comments and criticisms.—MICHAEL P. LOMBARDO, Dept. Biology, Livingston Coll., Rutgers Univ., New Brunswick, New Jersey 08903. Accepted 5 July 1982.

Infanticide by a Purple Martin.—Purple Martins (Progne subis) have been known to remove the young of other species from cavities (Nicholson, Auk 65:600–601, 1948), and they are capable of inflicting serious injury on other adults in intraspecific fighting (Brown, Bird-Banding 48:273, 1977). This note reports an instance of the killing of a brood of young Purple Martins by another female, a behavior not previously reported for this species.

The colony is an aluminum house with 12 cavities located in Jacksonville, Florida. On 12 May 1981, all cavities were occupied by Purple Martins, and cavity 86 contained four eggs. On 13 May, three eggs had hatched. The young developed normally for the first five days,
but on 18 May we noted that the young in this cavity had not gained as much weight as those in other nests. We noticed that the parents spent more time than others sitting outside the cavity. Subsequent events have shown that they were probably spending more time guarding the nest and less time feeding the brood than other pairs.

Both members of this pair were older birds. The male had full blue-black plumage and the female had extensive dusky coloration on the undertail coverts (North American Bird Banding Techniques, U.S. Fish and Wildl. Serv., Vol. II, Pt. 6, Species #611, 1977).

On the next day, 19 May, as we approached the colony, we found one young martin with its head crushed, lying on the ground about 10 m from the house. As we puzzled about this, we saw a young female (clear white undertail) fly in and perch outside cavity S6. She immediately began to fight with other adults perched on the house. Then we saw her reach into the cavity and pull a dead, young martin out onto the balcony. The other adults drove the female away, and we lowered the house. The dead chick had obviously been pecked to death. The skull was completely crushed and the head and back were lacerated with small round bruises. A search revealed the third young bird from S6, also pecked to death, on the ground about 12 m from the house. The young were marked, so we know that all three came from the same nest.

The female that originally occupied S6 was banded, but the young female that killed the brood was not. The unhanded female took possession of the cavity the day after the killings and took over the mate of the displaced female. (That it was the banded female’s mate was confirmed by checking his band.)

The new female began to lay her eggs in the cavity on 27 May. By 1 June, she had completed a clutch of six eggs. She incubated the eggs until 14 June when the nearly grown brood in cavity S4 began to leave their cavity and roam along the balcony intruding into other nests. By 17 June, all the eggs in S6 had disappeared or cracked. In houses with balconies, older broods invariably move from one cavity to another, sometimes trampling adjacent younger birds and eggs or depriving them of food (Bitterbaum and Brown, Nat. Hist. 90(5): 65–69, 1981). By 18 June, all birds of all age classes had left the house.

Among other swallows, infanticide has also been reported in the Tree Swallow (Iridoprocne bicolor). Shelley (Bird-Banding 5:134, 1934) observed a young female enter a colony in Massachusetts on 10 June 1934, and during the next 8 days kill over 19 nestlings from five broods. He saw another adult female kill three of what he presumed to be its own brood of five in the same colony. Kuerzi (Proc. Linn. Soc. N.Y. 52–53:1–52, 1940–41) found that young female Tree Swallows tended to be more aggressive than males or older females. He also noted that a late flight of young females and males passing through his Connecticut colony well after it was established each year caused much disturbance by fighting with the established pairs, but they were always driven away in the 3 years of his study. He did not observe any cases of infanticide.

Charles R. Brown (pers. comm.) tells us that in 13 years of intensive work with Purple Martins in Texas, he has found dead nestlings at times which seemed to have been pecked to death, but he does not know whether they were killed by House Sparrows (Passer domesticus), Common Starlings (Sturnus vulgaris) or other martins. At our colony, no species other than martins were seen near the house at any time.

For a late-returning bird, without a mate and with no place to nest, it seems that at least three reproductive options are available: (1) take over the cavity of another pair, try to find a mate, and rear a brood; (2) find another cavity that is not occupied, try to find a mate, and breed; (3) don’t breed. As for the second possibility, there was an empty martin house available, about 1000 m from the occupied colony. This house is made of wood and is not preferred by martins. It has been there for several years, but has never been used. Purple Martins are strongly attracted to the social stimulus of the colony and may require it to breed.
successfully (Brown, Auk 90:442, 1973). Whether or not unmated males were available is not known.

Our bird tried the first option. The failure of the new nest was due to the intrusion of older young, a situation made possible by the balconies on man-made martin houses. In the old woodpecker holes where martins originally nested, this would not have happened. It is important to remember that a tactic does not have to work every time to be advantageous. It is obvious that pushing into a colony is a better option than not trying to breed at all.

As Purple Martins do not recognize their own young (Bitterbaum and Brown 1981), this bird would probably not have recognized these nestlings as Purple Martins, but, of course, she would have recognized the parents. Therefore, it seems that there is no inhibition against infanticide in the social system of the Purple Martin.

Acknowledgments.—Our thanks to Eric Bitterbaum, Charles R. Brown, and David M. Niles for helpful comments and suggestions.—ROBERT W. LOFTIN and DON ROBERSON, Univ. North Florida, Box 17074, Jacksonville, Florida 32216. Accepted 20 May 1982.


Overlap of two broods of Eastern Bluebirds in the same nest and brood reduction.—Unusual nestlings among House Sparrows (Passer domesticus) in which eggs of the successive clutches were laid while young of the previous broods still occupied the nests have been reported (Lowther, Bird-Banding 50:160–162, 1979). I have made a similar observation for Eastern Bluebirds (Sialia sialis) wherein simultaneous use of a single nest box by two females suggests that nest-sites (boxes) are an important and limited resource for reproduction by Eastern Bluebirds. In association with this dual occupation of a single nest box I recorded brood reduction that encouraged speculation about infanticide.

Female R426 was caught and color-banded on 23 April 1979 at nesting territory 133 on a study site in Pendleton, Anderson Co., South Carolina. During that spring she and an unbanded male produced a five-egg clutch of which four eggs hatched and four young fledged on 16 and 17 May (Table 1). On 25 May a new, completed nest was found in the box and on 29 May female R426, again accompanied by an unbanded male, completed laying a four-egg clutch; all eggs hatched on 12 or 13 June. On June 16 I began to mark and weigh nestlings (Table 1). On 22 June I found one of the nestlings dead on the ground (Table 1). This was the only time I had seen a dead nestling so close to a nesting box containing live siblings. (I have found dead nestlings in the box with their live siblings and noted nestling disappearances attributed to parental removal. Dead nestlings found in the box were all more than 8 days old. Nestlings which have disappeared from a nest containing live siblings were all under 8 days old.) I did not see female R426 during my visit to the nest; she did not respond to a tape recording of bluebird song, although an unbanded male observed me from a perch about 10 m away. I did not see female R426 after 18 June. On 25 June I found color-banded nestling L573 dead just beneath the nesting box. The remaining nestlings, female L572 and male L574, appeared healthy and had normal weights on all days weighed.

In addition to the two nestlings remaining in the box, three eggs were also there on 25 June. Four eggs and two nestlings were in the box on 27 June. Female L229 was near the box with an unbanded male on 27 June and I frequently saw her on the territory during the remainder of the nesting attempt. (I caught and color banded female L229 on 26 May 1978 at a study site about 3 km from territory 133. During 1978, she and her mate, color-banded male R696, fledged nine young from two clutches.) The two remaining nestlings, the apparent offspring of female R426, fledged at a normal age between 28 June and 1 July. Only three
of the four eggs presumably laid by female L229 were consistently incubated; one was frequently found on the nest cup margin. Two of the four eggs hatched on 10 July. Female L229 and an unbanded male attended these nestlings, both of which developed normally and fledged before 2 August (Table 1).

Communal and cooperative nesting by these two females is an unlikely explanation for these observations because of the disappearance of one of the females. Nevertheless, kin-selected behavior is difficult to rule out. Because female R426 had disappeared by the time the eggs started to appear in the box with the nestlings, I am fairly certain that female L229 laid them. However, I do not know if these two females were related because each was caught and color-banded as an adult. It is possible, although I believe improbable, that the unbanded male with female L229 was unrelated to the nestlings, in which case the feeding of the two live nestlings by either or both the new female and the male might be attributed to altruism (Power, Science 189:142–143, 1975).

It is also possible, although improbable, that female L229 was attracted to the territory before female R426 was gone. Territorial males are able to attract more than one female to territories which contain more than one nest-site (Gowaty, unpubl.); however, there was only one box in this territory. The closest additional boxes were at least 50 m away and both were occupied. In addition, female-female aggression among Eastern Bluebirds can be fierce. I have seldom seen adult females tolerate other adult females in their territories (Gowaty, Anim. Behav. 29:1013–1027, 1981).

I think the most likely explanation for this overlap in reproductive events by two females is that female R426 died about 18 June. When female L229 was attracted to or discovered

<table>
<thead>
<tr>
<th>Date</th>
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<th>Parents: unbanded male and female L229</th>
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<tr>
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<tr>
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<td>hatch 6.5 17.5 24.0 ♀ fledged</td>
</tr>
<tr>
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<td>hatch 7.0 20.0 22.5 ♀ fledged</td>
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<tr>
<td>5/11</td>
<td>hatch 6.5 17.5 24.0 ♀ fledged</td>
<td>hatch 13.0 23.0 17.5 dead —</td>
</tr>
</tbody>
</table>

* Indicates unbanded individual.
a territory without an adult female resident, I think she fortuitously began a clutch in an already occupied box. This sort of opportunism may be an adaptive option for females of nest-site limited species such as bluebirds (Miller, Blue Jay 28:38–46, 1970; Zelany, The Bluebird, Indiana Univ. Press, Bloomington, Indiana, 1976). Intraspecific nest parasitism is not uncommon among bluebirds (Gowaty and Karlin, unpubl.) and also suggests the importance of nest-sites to females (Yom-Tov, Biol. Rev. 55:93–108, 1980). Access to nest-sites may be the single most important determinant of female breeding success among Eastern Bluebirds.

Although my observations are not extensive enough to discriminant amongst the explanations for brood reduction of the first female’s nestlings, it is possible that female L.229 killed the two nestlings that were found dead, thereby increasing the possibility that her own reproductive efforts would be successful. Such infanticide which makes critical resources available for reproduction by others has been described in langurs (Presbytis entellus) (Hrdy, The Langurs of Abu, Harvard Univ. Press, Cambridge, Massachusetts, 1977), lions (Leo leo) (Bertram, in Growing Points in Ethology, E. Bateson and R. Hinde, eds., Cambridge Univ. Press, Cambridge, England, 1976), and several other species as well. However, the first nestling was underweight (relative to its siblings) and the second lost weight markedly just before dying (Table 1), suggesting that they were not adequately fed after female R326 disappeared. Starvation might then be attributable to infanticidal through neglect by the father, siblicide through competition or harassment (Stinson, Evolution 33:1219–1225, 1979), or suicide (O’Connor, Anim. Behav. 26:79–96, 1978).—PATRICIA ADAIR GOWATY, Dept. Zoology, Clemson Univ., Clemson, South Carolina 29631. (Present address: Dept. Zoology, Univ. Oklahoma, Norman, Oklahoma 73109.) Accepted 15 June 1982.


Annual adult survival rates for Brown-headed Cowbirds wintering in southeast Texas.—For several years we have been studying the Brown-headed Cowbirds (Molothrus ater) which winter in large communal roosts in southeast Texas. One of us (KAA) has conducted a banding program in the vicinity of Bryan-College Station, Brazos Co., Texas, since 1969 (Coon and Arnold, N. Am. Bird Bander 2:7–11, 1977; Coon and Arnold, unpubl.: Arnold et al., unpubl.). The other (DMJ) has supervised studies of cowbird mortality at a roost on the Rice University campus in Houston, Houston Co., Texas (Good, Ph.D. diss., Rice Univ., Houston, Texas, 1979; Johnson et al., Auk 97:299–320, 1980; Johnson et al., The Ecology of Roosting Birds in Winter in Symp. Ecol. Soc. Am., in press). The roosts studied are near the southern limit of the winter range of M. ater (Meanley, U.S. Bur. Sport Fish. and Wildl. Resour. Publ. 100. 1971; Giltz and Burtt, Ecology of Roosting Birds in Winter in Symp. Ecol. Soc. Am., in press). Roost populations are usually composed of more than 70% males. We wished to know if cowbird mortality in winter in this region differed from that experienced by the whole population. Might migrating so far south provide an advantage due to mild winter weather, or a disadvantage resulting from migration? Might the preponderance of males in these roosts alter sex-specific survivorship?

The Bryan-College Station banding program for wintering cowbirds began in 1969 and has continued, essentially without interruption, through the 1980–81 season. The use of decoy traps and floodlight traps has resulted in banding over 75,000 cowbirds from 1969 through the 1976–77 season, the last year used in this analysis. Basically, all birds captured were banded and released. The sex ratios recorded in captured birds varied annually from more than 3:1 (males vs females) to in excess of 8:1 (males vs females) (Arnold et al., unpubl.). Recaptures suggest reasonable fidelity to wintering areas (Coon and Arnold, unpubl.).
Table 1

FREQUENCY OF RECOVERY OF DEAD COWBIRDS BY MONTH

<table>
<thead>
<tr>
<th>Month</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
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<td>29</td>
<td>7</td>
<td>36</td>
</tr>
<tr>
<td>Feb.</td>
<td>41</td>
<td>0</td>
<td>41</td>
</tr>
<tr>
<td>Mar.</td>
<td>30</td>
<td>2</td>
<td>32</td>
</tr>
<tr>
<td>April</td>
<td>20</td>
<td>3</td>
<td>23</td>
</tr>
<tr>
<td>May</td>
<td>14</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>June</td>
<td>6</td>
<td>1</td>
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</tr>
<tr>
<td>July</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Aug.</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Sept.</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Oct.</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Nov.</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Dec.</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Totals</td>
<td>150</td>
<td>20</td>
<td>170</td>
</tr>
</tbody>
</table>

Table 1 presents the seasonal distribution of band recoveries from dead cowbirds (150 males, 20 females) reported to the U.S. Fish and Wildlife Service Bird Banding Laboratory by persons other than the banders. Most recoveries were made between January and April, suggesting that winter is not a season of low mortality for these birds. The high percentage of males among these recoveries is to be expected, since males predominate in the population banded.

Table 2 (males) and Table 3 (females) summarize the survival times for birds banded during each roosting season in a form appropriate for calculating annual survivorship estimates. Since some of these must be considered incomplete data (i.e., we have not yet received all recoveries which will eventually result from some of the more recent banding seasons), we use the method derived by Haldane (pp. 454–458 in Proc. XI Inter. Ornithol. Congr., Basel, Switzerland, 1955) to calculate an estimate of annual survivorship based on all the data (complete and incomplete) for each sex. We base the distinction between complete and incomplete recovery data (9 years after banding for males, 6 years for females) on maximum longevities reported by Fankhauser (Bird Banding 42:36–42, 1971) which were greater than those included in our data (7.5 years for males, 4.8 years for females). The resulting estimates of survival rates (±SE) are: males—53 ± 3%, P(47% < S < 59%) = 0.95 and females—63 ± 7%, P(48% < S < 78%) = 0.95. The estimate of female survivorship is characterized by higher variance and is based on only 20 recoveries; both factors make its 95% confidence interval very broad.

Previously published estimates of Brown-headed Cowbird survivorship (or mortality) included different calculation methods and lacked estimates of variance. Therefore, we will conclude that they are significantly different from our estimates only if they are not contained within our 95% confidence intervals.

Fankhauser (1971) calculated weighted annual survival rates for Brown-headed Cowbirds banded in North America before 1 January 1960 and subsequently recovered dead through August 1965. Records for 195 male and 85 female cowbirds met his criteria that: (1) birds were at least 6 months old when recovered, and (2) recoveries were not influenced by the bander. Fankhauser’s estimates of annual survival rates were 48.5% for males and 40.4%
Table 2
Number of Male Brown-headed Cowbirds Banded During Successive Winter Seasons Which Were Recovered Dead Within Each One-year Interval (x) Following Banding

<table>
<thead>
<tr>
<th>Season banded</th>
<th>k&lt;sup&gt;a&lt;/sup&gt;</th>
<th>N&lt;sub&gt;k&lt;/sub&gt;&lt;sup&gt;b&lt;/sup&gt;</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969-70</td>
<td>11</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
</tr>
<tr>
<td>1970-71</td>
<td>10</td>
<td>45</td>
<td>20</td>
<td>9</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<td>—</td>
</tr>
<tr>
<td>1971-72</td>
<td>9</td>
<td>19</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Complete</td>
<td>Σ d&lt;sub&gt;x&lt;/sub&gt; = 69&lt;sup&gt;c&lt;/sup&gt;, d&lt;sub&gt;x&lt;/sub&gt; = 27</td>
<td>17</td>
<td>8</td>
<td>5</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>Σ (x - 1)d&lt;sub&gt;x&lt;/sub&gt; = 107</td>
<td></td>
<td></td>
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<tr>
<td>1972-73</td>
<td>8</td>
<td>20</td>
<td>10</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>1</td>
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<td>0</td>
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<tr>
<td>1973-74</td>
<td>7</td>
<td>23</td>
<td>9</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1974-75</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1975-76</td>
<td>5</td>
<td>35</td>
<td>18</td>
<td>16</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1976-77</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Incomplete</td>
<td>Σ n&lt;sub&gt;k&lt;/sub&gt; = 81, d&lt;sub&gt;x&lt;/sub&gt; = 39</td>
<td>25</td>
<td>7</td>
<td>9</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>Σ (x - 1)d&lt;sub&gt;x&lt;/sub&gt; = 70</td>
<td></td>
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<td></td>
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<tr>
<td></td>
<td>Σ k n&lt;sub&gt;k&lt;/sub&gt; = 150</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> k = maximum number of years of survival that could be recorded for individuals banded in each year.
<sup>b</sup> n<sub>k</sub> = number recovered dead that were banded in each season.
<sup>c</sup> d<sub>x</sub> = number recovered dead that had survived x years since banding.

For females. These estimates are both lower than our respective estimates, but only the one for females lies outside our 95% confidence intervals. Thus, we might conclude that female cowbirds wintering in southeast Texas have better annual survivorship than the average for all North America.

Table 3
Number of Female Brown-headed Cowbirds Banded During Successive Seasons Which Were Recovered Dead Within Each One-year Interval (x) Following Banding

<table>
<thead>
<tr>
<th>Season banded</th>
<th>k&lt;sup&gt;a&lt;/sup&gt;</th>
<th>N&lt;sub&gt;k&lt;/sub&gt;</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
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</thead>
<tbody>
<tr>
<td>1969-70</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<td>1970-71</td>
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</tr>
<tr>
<td>1971-72</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>—</td>
</tr>
<tr>
<td>1972-73</td>
<td>8</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
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<tr>
<td>1973-74</td>
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<td>4</td>
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<tr>
<td>1974-75</td>
<td>6</td>
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</tr>
<tr>
<td>Complete</td>
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<td>2</td>
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</tr>
<tr>
<td>1975-76</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>0</td>
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<td>1976-77</td>
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<td>—</td>
<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>Incomplete</td>
<td>Σ n&lt;sub&gt;k&lt;/sub&gt; = 4, d&lt;sub&gt;x&lt;/sub&gt; = 1</td>
<td>1</td>
<td>0</td>
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</tr>
<tr>
<td></td>
<td>Σ k n&lt;sub&gt;k&lt;/sub&gt; = 20</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Symbols are identified in Table 2.
Darley (Auk 88:560–566, 1971) (the only other published estimate of Brown-headed Cowbird survivorship) based his study on a local breeding population in Ontario. Darley estimated survivorship as the percentage of birds banded one year that returned to breed in the same area the following year. He estimated 62% survivorship for adult males and only 45% for adult females, based on 60 and 40 initially banded birds, respectively. Male survivorship is greater than, and female survivorship less than our estimates for southeast Texas.

Our estimates of annual survivorship rates for cowbirds that winter in southeast Texas tend to be greater than Fankhauser’s (1971) estimates for the North American population as a whole. This difference is slight (and not significant) for males, but it is great (and highly significant) for females. Thus, we might conclude that migrating farther south confers some survival advantage, especially for females. We find it especially interesting that these females appear to experience considerably better survivorship than the males with whom they roost in the winter (63 vs 53%), when both Fankhauser (1971) and Darley (1971) reported lower female survivorship. Our results are consistent with the observation (Johnson et al., 1980) that mortality experienced in the Houston roost was due to food-limitation, and tended to affect males more than females in some years. Perhaps some as-yet-unidentified difference in foraging behavior, related to sexual dimorphism in size, causes the minority sex (females in southeast Texas roosts) to experience less competition for food and enjoy better survival.

We thank William E. Grant and R. Douglas Slack for comments on the manuscript. This is contribution TA 16971 from the Texas Agricultural Experiment Station.—KEITH A. ARNOLD, Dept. Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843, AND DAN M. JOHNSON, Dept. Biological Sciences, East Tennessee State Univ., Johnson City, Tennessee 37614. Accepted 20 Apr. 1982.


Flocking pattern of foraging American Crows in Oklahoma.—Field studies of American Crows (Corvus brachyrhynchos) outside the breeding season have concentrated upon the large communal roosting sites that these birds use during the winter (e.g., Kalmbach and Aldous, Wilson Bull. 52:198–206, 1940; Haase, Ohio J. Sci. 63:145–151, 1963). The implication from those studies is that the roosting flock is the social unit for the species at this time of year, and that birds disperse broadly to forage. Two hypotheses have been proposed as to how crows may find food when leaving the roost. The first maintains that birds are attracted to birds already foraging. Hinde (pp. 373–411 in Biology and Comparative Physiology of Birds, A. J. Marshall, ed., Academic Press, London, England, 1971) referred to this process as foraging by “local enhancement.” The alternative hypothesis is that the roost serves as a “center” (Ward and Zahavi, Ibis 115:517–534, 1973) where birds obtain information about the location of food resources nightly, and then fly to sites having greatest availability of food resources the following morning. A recent study (Loman and Tamm, Am. Nat. 115:285–289, 1980) inconclusively addressed these theories relative to food finding by Hooded Crows (C. cornix) and Common Ravens (C. corax). From November 1977 through September 1978 we monitored the size of flocks of foraging crows in north-central Oklahoma and observed habits of those flocks. The observations lead us to speculate that the social unit of American Crows is the family throughout the year, and raise some doubts about the dependence of crows upon either of the two approaches to locating food resources during winter as proposed by Hinde (1971) and Ward and Zahavi (1973).

We recorded the location and flock size of all crows observed foraging between 08:00 and 16:00 within a 25-km radius of Stillwater, Payne Co., Oklahoma, 1 November 1977–30 September 1978. Most crows foraged in rangelands within 10 km of a roost-site located 13 km
due east of Stillwater. Occasionally crows foraged in riparian or oak (Quercus spp.) woodlands. We do not include those flocks herein as we were unsure that we saw all birds in a flock.

Crows migrated into Oklahoma in large numbers during October 1977. An estimated 300–400 crows used the communal roost-site that winter. This site was located in cottonwood trees (Populus spp.) along an intermittent stream. Birds usually dispersed from the roost in varied directions shortly after first light each morning. They generally began foraging on the ground about sunrise.

Relative to the larger communal roost, crows foraged in small flocks. Flocks observed 1 November–31 January ranged from 1–9 individuals with 119 of 144 (82.6%) comprising 3–6 birds. Mean flock size was 4.1 ± 0.13 birds. From late morning through the remainder of the day crows appeared to spend less time foraging. By mid-afternoon they began concentrating in larger, nonforaging groups (secondary roosts), usually in trees, prior to moving back to the communal roost at sundown.

We continued to monitor flock sizes of foraging crows through the nesting season and summer of 1979. Birds began to appear more frequently in flocks of two (pairs?) about mid-February and mean flock size reached a minimum in May (Fig. 1). Nesting activities occur 5 March–31 May in Oklahoma (Sutton, Birds of Oklahoma, Univ. Oklahoma Press, Norman, Oklahoma. 1967). Flock size increased markedly in June, and gradually thereafter through September.

Crows remain in family units after fledging (Good. The Life History of the American Crow Corvus brachyrhynchos Brehm, Ph.D. thesis, Ohio State Univ., Columbus, Ohio. 1952) at least until that time when they leave the breeding grounds (D’Agostino et al., Wilson Bull. 93:394–395, 1981). We attribute the dramatic increase in flock size of Oklahoma crows in

Fig. 1. Mean (±SE) flock size of foraging crows in north-central Oklahoma, November 1977–September 1978. Respective sample sizes are given on the figure.
June to the presence of fledglings accompanying their parents to the foraging sites. As mean flock size of birds that bred in Oklahoma was comparable in September to what we saw among migrants during the previous winter, we hypothesize that at least some young spend their first winter with their parents.

Our hypothesis is supported by additional observations. Flocks of foraging crows often had the same number of individuals within the same vicinity for 2–20 days consecutively, as if on a winter territory. Two such flocks (of four and five individuals, respectively) were noted repeatedly about 0.5 km apart in a field along a highway over the course of 9 days in mid-January. On the ninth day we watched the flock of four fly into a cottonwood tree within 50 m of where the flock of five was foraging on the ground. The flock of five immediately flew to the tree, and all nine crows fought noisily for about 15 sec. After the interaction the crows left the site in two flocks (four and five individuals) in opposite directions. On subsequent days only a flock of five was present in that vicinity. Finally, we noted that during the winter many (48 of 144, 33.3%) flocks of foraging crows were accompanied by 1–2 sentinel birds. D’Agostino et al. (1981) recently proposed that sentinel behavior by American Crows was an extension of parental care.

From these observations we infer that the basic social unit of nonbreeding crows may be the family and not the roost as implied by theories proposing information exchange about the location of food resources. Family relationships may be obscure where crows winter in large roosts and also forage in large flocks. However, large roosts in Oklahoma occur in areas of abundant, localized foods in the form of cultivated crops (grains, pecans, etc.) produced by intensive agricultural practices (Aldous, J. Wildl. Manage. 8:290–295, 1944). Our observations were of a smaller roost in native grassland/savannah habitats with negligible tillage. Whereas crows may follow other birds (share information) from large roosts to feeding sites or be attracted to birds already foraging (local enhancement) in areas of abundant or concentrated foods, in native landscapes the roost appears to serve some other (thermoregulatory, antipredator, etc.) functions (Broom et al., Bird Study 23:267–279, 1981) which seem inherent to the roost-site itself.


An additional method of foraging in litter by species of Turdus thrushes.—Although ground-foraging birds often feed directly from the surface, many also excavate the litter in one or more distinct ways to uncover hidden food. For example, unilateral (single) scratchers use one leg at a time to move litter, e.g., many gallinaceous birds and Caracaras (Polyborus) (Brown and Amadon, Eagles, Hawks and Falcons of the World, Vol. 2, McGraw-Hill, New York, New York, 1968; pers. obs.). In contrast, bilateral (double) scratchers displace the litter in a backward jump using both feet simultaneously, e.g., in many American emberizines (Greenlaw, Condor 79:426–439, 1977). Bill-sweepers such as jays (Cyanocitta) and thrashers (Toxostoma) move litter with sideways sweeps of the bill (Clark, Wilson Bull. 83:66–73, 1971).

At least two avian genera employ either bill-sweeping or bilateral scratching. Egyptian Plovers (Pluvianus aegyptius) use bilateral scratching and bill-sweeping at different times
Table 1
Numbers of Observations of Kinds of Terrestrial Foraging by Species of Turdus

<table>
<thead>
<tr>
<th>Species</th>
<th>No. excavation</th>
<th>Bill-sweeping</th>
<th>Bill-sweeping plus unilateral scratch</th>
<th>Bill-sweeping plus bilateral scratch</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eurasian Blackbird</td>
<td>562</td>
<td>354</td>
<td>2</td>
<td>60</td>
<td>978</td>
</tr>
<tr>
<td>Redwing</td>
<td>24</td>
<td>6</td>
<td>0</td>
<td>2</td>
<td>32</td>
</tr>
<tr>
<td>Song Thrush</td>
<td>238</td>
<td>52</td>
<td>0</td>
<td>3</td>
<td>293</td>
</tr>
<tr>
<td>Mistle Thrush</td>
<td>68</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>73</td>
</tr>
<tr>
<td>American Robin(^a)</td>
<td>96</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>103</td>
</tr>
</tbody>
</table>

\(^a\) Data from 15 March–17 June 1979 in Connecticut.


From 30 June 1979 through 23 June 1980 I observed unmarked wild Turdus around Reading, Berkshire Co., England. I had previously seen bill-sweeping by the Eurasian Blackbird (*T. merula*) (Clark 1971). This species, on occasion, also excavates with a foot; Witherby et al. (The Handbook of British Birds, Vol. 2, Witherby, London, England, 1938) mentioned without further detail the occasional use of the feet in foraging, and Snow (A Study of Blackbirds, Allen and Unwin, London, England, 1958) noted briefly the use of a unilateral scratch simultaneously with bill-sweeping. Throughout the year I saw blackbirds using the bilateral scratch synchronously with bill-sweeping (Table 1). In this method the entire body moves backward while the head sweeps to the side as the birds excavate concavities up to 2.5 cm deep in litter, particularly in woods. Only twice (2 July and 13 December) did I detect unilateral scratching together with bill-sweeping as mentioned by Snow (1958); hence the bilateral scratch appears to be far more common than the unilateral one. Bilateral scratching never occurred without synchronous bill-sweeping, and the bill consistently displaced more litter than did the feet.

The foraging method used appeared to be associated in part with the depth of the litter. On litter-free lawns blackbirds often captured earthworms and arthropods by pecks or stabs. Bill-sweeping without foot excavation was often used on shallow litter (e.g., scattered leaves on a lawn), whereas both bill and feet were often used in deep litter in wooded sites. Here excavation was prolonged, frequently lasting for many seconds.


Only after 8 months of watching did I see Song Thrushes (*T. philomelos*) bilaterally scratching while bill-sweeping; on 5 March one bird repeatedly did this, and one, possibly the same individual, did it twice on 19 March. Henty (Wilson Bull. 88:497–499, 1976) previously reported bill-sweeping by captive Song Thrushes as well as the occasional use of the unilateral
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only have have am review watched. October—would saw Clark usually species (1978) June reported of Wilson. However, I have seen this behavior in blackbirds, Redwings, and Song Thrushes, though only when synchronous with bill-sweeping. Considering the apparent rarity of this behavior in Redwings and Song Thrushes it would be premature to conclude from the absence of records for the Mistle Thrush and American Robin that such species entirely lack this behavior.

At Reading I saw bill-sweeping performed by five other species that fed in some of the same sites used by the Turdus thrushes: Common Gallinule (Gallinula chloropus) on 8 February and 12 March, Magpie (Pica pica) on four occasions from 1 October–31 March, Dunnock (Prunella modularis) on four occasions from 3 December–9 April, European Robin (Erithacus rubecula) on 22 January, and Great Tit (Parus major) on four occasions from 15 December–9 April. On numerous other occasions these five species fed directly from the surface of the ground.

Bill-sweeping has apparently not been previously reported for Common Gallinules but has been seen regularly in Magpies (Clark 1971) and exceptionally in Dunnocks (Caldow, Br. Birds 67:516, 1974; Goodwin, pers. comm.), European Robins (Goodwin, pers. comm.), and Great Tits (Perrins, British Tits, Collins, London, England, 1979:136).

Acknowledgments.—I thank D. M. Broom and D. Goodwin for helpful information and Prof. K. Simkiss for providing facilities at the University of Reading.—GEORGE A. CLARK, JR., Biological Sciences Group, Univ. Connecticut, Storrs, Connecticut 06268. Accepted 22 June 1982.


Northern Mockingbird kills Cedar Waxwing.—Northern Mockingbird (Mimus polyglottos) defense of winter territories, usually centered on fruit-bearing trees or shrubs, has been well documented. In California, Michener and Michener (Condor 37:97–140, 1935) reported vigorous defense of date palms (Phoenix sp.), hawthorn (Crataegus sp.), and persimmon (Diospyros sp.). Similar behavior has been reported in defense of hollies (Ilex sp.) in South Carolina (Moore, Behav. Ecol. and Sociobiol. 3:173–176, 1978) and pyracantha (Pyracantha sp.) shrubs in North Carolina (Stewart, J. Field Ornithol, 51:375, 1980). Moore (1978) concluded that the aggressiveness of the defending mockingbird was directly proportional to the degree of frugivory of the intruding species. He recorded the highest aggression index (proportion of intrusions repulsed) for the Cedar Waxwing (Bombycilla cedrorum), a species dependent almost wholly on fruits in the winter (Martin et al., American Wildlife and Plants: a Guide to Wildlife Food Habits, Dover Publications, Inc., New York, New York, 1951:158). Moore indicated, however, that physical clashes were infrequent. We report here a physical clash carried to the extreme.

Our observations focus on a small cherry-laurel (Prunus caroliniana) tree located on our office grounds in the city of Montgomery, Montgomery Co., Alabama. This particular tree is usually fruit-laden in the winter and has, in the past, been visited regularly by flocks of
Cedar Waxwings that often completely strip the tree of fruit in a matter of hours. In late February 1981, we noticed that almost none of the fruit had been used. One afternoon several days later, we saw an aerial clash near the fruit tree between a mockingbird and Cedar Waxwing. The mockingbird pursued and forced the Cedar Waxwing to the ground in a small planter where it pinned the waxwing and repeatedly struck the other bird with its bill, killing it. When we went to retrieve the dead bird, we found another Cedar Waxwing lying dead nearby. Both birds had several similar wounds on their backs. None of the wounds showed any evidence of skin puncture but each was marked by subcutaneous bleeding. In January 1982, we found another dead Cedar Waxwing with a shallow puncture wound on its dorsum lying within 15 m of the cherry-laurel tree. We cannot with certainty attribute the demise of the latter two waxwings to mockingbird aggression, since we were not witness to either of their deaths. However, the similarities of the wounds and the proximity of the dead birds to the fruit tree lead us to strongly suspect it.


American Coot apparently suffocates while attempting to swallow lizard.—On 14 February 1981, along the shoreline of San Pablo Reservoir (approximately 30 km northeast of San Francisco, Contra Costa Co., California) at 13:00 I discovered a dead American Coot (Fulica americana) lying face down in shallow water in a small inlet. A dead western fence lizard (Sceloporus occidentalis), 16.5 cm in length, had one-third of its body lodged head first in the coot’s gullet. The plumage of the coot was still normally waterproof, its eyes were open and glossy, and rigor mortis was not complete. An autopsy was performed on the coot and the cause of death appeared to be suffocation (with verification from Howard Brooks-Korn, D.V.M.). The lizard was blocking the glottis, cutting off air to the lungs. The raised scales of the lizard may have prevented the coot from regurgitating the lizard. It appears the lizard did not try to bite or hold onto the inside of the coot’s mouth. The coot’s physical appearance seemed normal and no indication of starvation was noted. Opening of the gizzard (the esophagus was empty) revealed fragments of grass and sand. A search of literature yielded only one pertinent paper (Jones, Food Habits of the American Coot with Notes on Distribution, Wildl. Resear. Bull. No. 2, Bur. Biological Survey, U.S. Dept. Interior, 1940) which mentions salamanders and other amphibia in the diet. No previous mention of predation on lizards was found, but fish are taken (Jones 1940).

Acknowledgments.—For assistance with this manuscript, I am grateful to Dr. Brooks-Korn, Dr. F. A. Pitelka, Dr. J. D. Rising, Dave Garcelon and Pam Nave.—Gary F. McCurdy, 119 Las Vegas Rd., Orinda, California 94563. Accepted 10 Apr. 1982.


Head-scratching method of Galapagos finches unaffected by variation in cranial morphology.—The head and bill of Darwin’s finches (Geospizinae) have undergone rapid and extensive morphological change (Grant, Am. Sci. 69:653–663, 1981). Thus, the Geospiz-
Table 1
HEAD-SCRATCHING IN THE GEOSPIZINAE

<table>
<thead>
<tr>
<th>Species</th>
<th>Overwing head-scratches</th>
<th>Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small Ground Finch (Geospiza fuliginosa)</td>
<td>1 (1)*</td>
<td>Rabida</td>
</tr>
<tr>
<td></td>
<td>2 (1)</td>
<td>Santa Fe</td>
</tr>
<tr>
<td></td>
<td>2 (2)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Medium Ground Finch (G. fortis)</td>
<td>1 (1)</td>
<td>Isabella</td>
</tr>
<tr>
<td></td>
<td>3 (1)</td>
<td>Santiago</td>
</tr>
<tr>
<td></td>
<td>4 (3)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td></td>
<td>1 (1)</td>
<td>Santa Maria</td>
</tr>
<tr>
<td>Cactus Finch (G. scandens)</td>
<td>1 (1)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Vegetarian Finch (Platyspiza crassirostris)</td>
<td>2 (1)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Small Tree Finch (Camarhynchus parvulus)</td>
<td>3 (2)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Large Tree Finch (C. psittacula)</td>
<td>2 (1)</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Warbler Finch (Certhidea olivacea)</td>
<td>1 (1)</td>
<td>Santa Cruz</td>
</tr>
</tbody>
</table>

* The number of observations is followed (in parentheses) by the minimum number of individuals observed.

The Geospizinae are an ideal group within which to study potential morphological correlates of avian head-scratching methods. Birds head-scratch by raising the foot dorsal to the lowered wing (overwing or indirect) or by passing the foot ventral to the folded wing (underwing or direct). The method employed is usually common to all individuals of a species (Simmons, Ibis 103A: 37-49, 1961), although some intraspecific variation exists (Dunham, Auk 80:375, 1963; Burtt and Hailman, Ibis 120:153-170, 1978; Burtt, Ibis 122:541, 1980). Most intraspecific variation (e.g., the ontogenetic shift from underwing to overwing head-scratching) and most taxonomic variation (e.g., most non-passerines use the underwing method of head-scratching) suggest that overwing head-scratching is the derived method. Nonetheless, anomalous data persist (e.g., Burtt 1980) and the evolutionary significance of avian head-scratching methods remains unresolved. Hence, I observed head-scratching among Darwin’s finches, a subfamily whose evolutionary relationships and morphology have been particularly well studied.

Observations made during a week’s visit to the Galapagos Islands in early December 1980 were often with the unaided eye, although 8 × 32 binoculars were used whenever necessary. Because several species vary morphologically from island to island (Lack, Darwin’s Finches, Cambridge Univ. Press, Cambridge, England, 1947), I have grouped the data for each species by island.

Among the Geospizinae observations of seven species in four genera showed that all adults head-scratched over the wing (Table 1). There was no variation among genera, among species, among individuals on the same or different islands or habitats (e.g., the Small Ground Finch [Geospiza fuliginosa], Medium Ground Finch [G. fortis]), or among successive head-scratches of the same individual; six of the 16 finches I observed head-scratched more than once.

The basic problem is why some birds head-scratch over the wing and others head-scratch under the wing. The alternatives are that head-scratching method is evolutionarily conservative, a phylogenetic legacy that parallels taxonomy, or that head-scratching method is evolutionarily labile, in which case it varies with ecology, other behavior, or anatomy. My data indicate that among the Geospizinae, head-scratching method is evolutionarily conservative. Galapagos finches head-scratch over the wing as do other fringillids (Andrewr, Br. J.

I thank A. J. Gatz, Jr., T. C. Grubb, Jr., and G. M. Fails for their comments on earlier drafts. Preparation of the manuscript was supported by an Ohio State University Postdoctoral Fellowship and NSF grant DEB 721014.—EDWARD H. BURTT, JR., Dept. Zoology, The Ohio State Univ., Columbus, Ohio 43210. (Present address: Dept. Zoology, Ohio Wesleyan Univ., Delaware, Ohio 43015.) Accepted 20 Apr. 1982.


**Hermit Thrush nesting on a rock face.**—While conducting population studies of birds near Walker Lake, Regional Municipality of Muskoka, in central Ontario (45°21′N, 79°06′W), we observed an unusual nesting of a Hermit Thrush (*Catharus guttatus*) on a small rock face in a mature eastern hemlock (*Tsuga canadensis*) forest. The local terrain sloped steeply to the lakeshore, with many small rock faces and large boulders.

On 8 June 1977, an adult Hermit Thrush was flushed from the rock face by the senior author. This vertical rock face was approximately 2.25 m high, and faced west. Upon examination, an empty, weathered nest was located on an open ledge. An adult Hermit Thrush was observed on 14 June 1977 on another nest with four eggs located less than 1 m from the first nest, in a rectangular-shaped cavity situated 1.5 m up the near-vertical rock face. The cavity was 30 cm wide, 12 cm high, and extended 21 cm back into the rock. The active nest was directly adjacent to another more weathered but otherwise similar nest and together both nests filled the width and depth of the cavity. All three nests were comprised of bark, twigs and moss, and lined with pine needles, typical of *C. guttatus* (Harrison, A Field Guide to Birds’ Nests, Houghton Mifflin Co., Boston, Massachusetts, 1975). The cup of the nest in use was 8 cm in diameter, and was entirely protected from above by the rock. Only a portion of the outer edge of the nest was exposed, and grass was growing along this edge. There was a space of approximately 6 cm between the top of the nest and the overlying rock. This particular nesting attempt was unsuccessful.

During August 1978 the nest-site was again examined. The previously weathered nest within the cavity had been refurbished, indicating possible reuse by Hermit Thrushes during the 1978 nesting season.

Hermit Thrushes typically nest in sheltered locations on the ground and occasionally in trees (Godfrey, Natl. Mus. Can. Bull. No. 203, 1966; Harrison 1975). The average height of tree nests is 0.6–1.2 m (Harrison 1975). Bent (U.S. Natl. Mus. Bull. 196, 1949) reported one instance of a Hermit Thrush nesting on an exposed rock shelf, but stated that the nest is generally built in a “natural depression of a knoll or hummock, forming a kind of protective canopy over the nest [Bent 1949:145].” The thrushes involved in our observed nesting attempts were apparently responding to the shelter offered by the crevice in the rock face.

The location of all three nests within a horizontal distance of 1 m, and the reuse of at least one nest, suggest that this may be a fairly typical nesting practice, or that the same thrush(es) may have returned to the same territory and the same nest-site for possibly 3–4 breeding seasons (pre-1977, 1977, 1978). Although banding returns would be required to verify this, our observations suggest that individuals of *C. guttatus* may reuse nests.—EDWARD R. ARMSTRONG, Ministry of Natural Resources, P.O. Box 730, Cochrane, Ontario P0L 1C0, Canada, and DAVID L. EULER, Ministry of Natural Resources, Wildlife Branch, Whitney Block, Queen’s Park, Toronto, Ontario M7A 1W3, Canada. Accepted 23 Aug. 1982.
ORNITHOLOGICAL LITERATURE

THE COTINGAS. By David Snow, illustrations by Martin Woodcock. Cornell University Press, Ithaca, New York, 1982:203 pp., 21 color plates, 15 figs., 30 maps. $45.00.—For the first time, comparative information on the biology of all members of the family Cotingidae (sensu lato) is assembled in a single volume. The book commences with a general account of the origin, evolutionary history, natural history, morphology, and classification of the group—no easy task for so heterogeneous a collection of species. There follows a series of species accounts with a separate chapter for each genus. The information is organized under a variety of headings to cover classification, species limits, distribution (with maps and Hafferian scenarios), habitat, food, behavior, breeding and molt cycles, physical features, weight and other measurements, and geographic variation. The section headings are not strictly comparable from one generic account to the next, undoubtedly because the information has been compiled from various published and unpublished accounts and is not itself always comparable; this variability impairs cross reference very little. A useful section on the derivation of the scientific names of the cotings is included as an appendix. All species are accurately illustrated in full-page color plates by Martin Woodcock, a feature that greatly enhances the book’s value as a very convenient reference.

The completeness of the species accounts varies a great deal depending on existing knowledge, and Snow suggests intriguing possibilities for further fieldwork. He remarks, for example, on the incompletely known breeding behavior of the Swallow-tailed Cotinga (Phibalura flavirostris). Some unpublished observations suggest that in this species the female may lay a clutch of eggs in each of the two nests, with her mate tending one nest and herself the other. If confirmed this would constitute the only known instance of such a breeding strategy in passerines. A further example of the patchiness of knowledge of cotingid species is the Kinglet Calyptura (Calyptura cristata), a bird that apparently has not been seen at all in this century. Some of the more complete comparative accounts include that of the four species of Procnias, from Barbara Snow’s extensive work, and of the two species of cock-of-the-rock. The latter is enhanced by the contribution, heretofore unpublished, of detailed field observations on the courtship display of the Andean species.

The sequence of genera in this volume differs somewhat from that employed by Snow (1973) and adopted for use in volume 8 of the Peters Checklist. The latter sequence is essentially that of Sclater (1888), based on tarsal scutellation and degree of syndactyly, although some changes have been made on the basis of syringegal morphology (Ames 1971) and distribution, and several genera have been placed in other families subsequent to Sclater’s (1888) work. Snow has here incorporated into his classification some of Warner’s (1965) conclusions from unpublished work on the cranial osteology of the Tyrannoidea, resulting in slight alteration of the generic sequence from that published in the Peters Checklist in 1979.

As Snow points out clearly, the classification of the suboscines is controversial. It is based on a wide variety of characters, analysed in no particular way and mysteriously acquiring “generic rank” or “familial rank.” Rarely has any attempt been made to determine whether these characters are primitive or derived for the group in question. In 1876 Garrod reported that in the cock-of-the-rock (Rupicola crocea (=rupicola)), the main artery of the thigh is the sciatic (=ischiatric), whereas in the one piprid and seven cotingid genera that he examined the main artery is the femoral. This has since been widely cited and has contributed to the placement of Rupicola in its own family in some classifications; in other words the ischiatric artery is used as a “familial character” for the Rupicolidae. Garrod (1876) also pointed out, however, that in all the tyrannids and pitittids and the hundred or so oscines he dissected, the ischiatric artery is also the main artery, and Midgård (1982) has found this to be true as well.
in 15 of 16 avian orders examined. The femoral artery is probably a derived condition clustering as a monophyletic group those forms in which it is important, and that in *Rupicola* the ischiatic artery is the main one tells us only that it is not a member of that group. Interestingly, one of the species found by Garrod to possess this modified femoral artery is *Tityra personata* (=*semifasciata*), yet the Peters Checklist places *Tityra* (and *Pachyramphus*) as a subfamily of the Tyrannidae because they “have essentially Tyranno-Myiarchine skulls” (Traylor 1977) while differing from all tyrannids in several (derived?) cranial characters. It seems that on the basis of the thigh artery *Tityra* is a cotingid, and on the basis of cranial osteology it is not quite a cotingid and not quite a tyrannid. Snow stresses the heterogeneity of the Cotingidae (s.l.) and the likelihood that the family is not monophyletic; I should think that the inclusion in the Cotingidae of *Tityra* with its femoral artery could only raise the family standards. Although the book is not primarily a systematic study, the classification used determines what species are included, and I am disappointed in the omission from Snow’s book of some interesting forms. Clearly, more work is needed to solve such problems with careful phylogenetic character analyses. Snow greatly facilitates and encourages this task by summarizing the available information from his own and others’ work, reviewing the literature, and underscoring the gaps in our knowledge of the Cotingidae. His book is an indispensable reference and an important contribution to the ornithological literature.—Mary C. McKitrick.


**SONGS OF THE VIREOS AND THEIR ALLIES.** By Jon C. Barlow, narrated by J. W. Hardy. Ara Records. 1615 N. W. 14th Ave., Gainesville, Florida 32605, 1981. Two phonodiscs. $12.00—This album results from the happy collaboration between the eminent authority on vireos (Barlow) and the leading expert on the technology of avian sound recording (Hardy). Known or presumed primary songs of 39 of the 43 species in the family are represented. Of the 68 cuts (a cut is a single sequence of recorded vocalizations of a particular taxon), 42 were obtained by Barlow himself, reflecting his extraordinarily broad geographic and taxonomic familiarity with the Vireonidae. The sequence of subfamilies follows the treatment of E. R. Blake in Peters’ Checklist of Birds of the World (R. A. Paynter, Jr., ed., 1968, Vol. XIV:103–138). Within subfamilies, cuts of vocalizations of species and of subspecies are arranged from simple to complex, and according to Barlow’s preferred sequence of phylogenetic relationships. This renders simple the vocal comparison of closely-related taxa, a boon to systematists and recreational birders alike.

Barlow’s text on the reverse side of the record jacket provides an excellent overview of
the Vireonidae. These liner notes cover distribution, habitat, and general body size but mostly describe the vireo songs themselves in a useful comparative synthesis. For each of the 68 cuts, the scientific and common names of each taxon, date of recording, general locality, and name of recordist are also given on the record jacket. This information is narrated in full by J. W. Hardy prior to each cut on the actual records. The technical aspects of the production reach a high level. Not only are most of the recordings virtually free of background noise but the narration by Hardy is clear and eloquent. The faint buzzing of flies on a few cuts serves to remind those who have labored to obtain high-quality recordings of avian vocalizations in humid places that this goal is seldom reached in comfort.

As Barlow states in the jacket notes, vireos are rarely beautiful singers; instead, the repetitiveness of notes or phrases is their hallmark. Moreover, in the author’s words, one is “struck further by both the loudness and persistence [sic] of their song.” Listening to all these recordings at a single audition, one is also impressed by the fundamental similarity of the harsh whistles, chirps, slurs, and vibratos sung by many forms. This is especially evident among the numerous members of the genus Vireo, where interspecific differences in tempo of delivery of syllables of the same basic quality and form may serve importantly in reproductive isolation. Only the bizarre police-whistle trill of the Blue Mountain Vireo (Vireo osburni) of Jamaica stands out from the vocalizations of its congeners, and even this song resembles uncommon trills in the general repertoires of the Yellow-throated Vireo (V. flavifrons) and Solitary Vireo (V. solitarius).

Barlow properly acknowledges the considerable aid received from some 21 collaborators who either sent tape recordings unrepresented in his large personal collection, assisted in the fieldwork, or helped in the preparation of the first master tapes on which the records were based. A fine pen-and-ink drawing of a Black-capped Vireo (V. atricapillus) on a spray of oak, by Nancy Halliday, graces the record jacket.

Overall, this is a high-quality production, prepared with care, class, and competence, and deserving to be widely heard and appreciated. Barlow and his collaborators are to be praised for their fine addition to the small but growing library of avian vocal anthologies.—NED K. JOHNSON.

INSTINCTIVE NAVIGATION OF BIRDS. By Edward C. Gerrard. The Scottish Research Group, Skye, Scotland. 1981:185 pp., numerous maps and drawings. Price not given.—The field of bird navigation has made exceptional advances in the last decades due to the hard work and clear thinking of a few biologists such as Gustav Kramer, Donald R. Griffin, and William T. Keeton. The work of these and other dedicated men and women has accumulated massive banks of experimental and observational evidence about the depth and breadth of the navigational abilities of birds. E. C. Gerrard was stimulated by the reports of this research, and his response was to share his thoughts by presenting them in the form of a privately published book. The book is not strictly about bird navigation; rather, it is a collection of thoughts by someone who is interested in the concepts of bird navigation from a theoretical point of view. Undoubtedly, there is room for careful and objective theoretical analysis of the bird navigation data collected thus far, for the scientific data are extensive. For example, the catalog of summaries of the homing pigeon experiments performed by Keeton’s group at Cornell is over 900 pages long, and the test summaries of the past 14 years are now available from the Cornell Laboratory of Ornithology as a computerized data bank on 28 magnetic discs. Surely in these data some new conclusions and concepts remain to be discovered.

Unfortunately, the analysis by Gerrard is neither careful nor objective. It omits key experimental data, and it reports incorrectly the results of experimental and observational
studies. For example, Gerrard states (in Appendix I: Some pigeon homing feats examined) that homing pigeons can return home only from either the north or the south but not from the east or the west, and that homing pigeons cannot return home from unfamiliar territory. He also states (p. 22) ". . . I defy anyone to take large numbers [of pigeons] to release points in all directions and release them 100 miles from home (in overcast or sunny conditions) and get every bird to fly straight home even if they are highly trained. . . ." But pigeons can home from all compass directions, and it has been clearly documented that they can home from unfamiliar territory. Furthermore, these abilities were demonstrated by transporting thousands of homing pigeons in all directions and releasing them (under overcast and sunny skies) from distances of both less than and more than 100 miles. Data from thousands of tests are available, and the results are the opposite of what Gerrard supposes. The results of this careful work are published in readily obtainable scientific journals. But rather than use the scientific literature or the new computer data banks, Gerrard has based many of his criticisms on information from television programs or outdated army reports from the 1940's.

Gerrard has proposed a method of maintaining straight-line flight that does not invoke the sun or star compass. (Most of the mechanisms that constitute his method have been proposed before, although Gerrard does not acknowledge this.) Gerrard does not recognize the complexity of the behavior of migratory birds, and therefore he has formulated an orientation model based on combining two optical cues, with the thought that this might offer a more parsimonious explanation of bird navigation than the sun compass model. His concept is that in the morning birds could use low-angle reflected glare from the surface of water; then at some appropriate time, the birds would switch to a constant sun angle for most of the day; and in the evening they would again revert to low-angle glare as the constant angle (menotactic) reference. His model generates a flight path consisting of three looping segments per day, and he believes this path might be misinterpreted as a straight-line sun compass course. Whether all this is more or less complex than ordinary sun compass behavior is a matter of personal opinion; but ultimately, the navigational mechanisms the birds are using are to be found in the birds, not in theoretical models. It is our job to try to find out what the animals are really doing, not to construct a series of rational deductions that contradict the empirical evidence.

The sun compass is one of the most thoroughly studied animal orientation mechanisms: using a sun compass, the animal pursues a constantly changing angle between the straight path of travel and a celestial landmark, such as the sun or a group of stars. Simpler models than the sun compass have been considered by some workers who have suggested that birds or insects fly in daily, semicircular, looping paths by keeping a constant angle between the flight heading and the sun or star pattern, but the predicted looping paths were not observed to occur. Lacking confirmation, the idea has been discarded by most investigators.

Gerrard's theories rely heavily on the use of visible cues near the horizon to explain much of the behavior of migratory birds. Optical orientation to cues near the horizon has been observed and studied before. Orientation to sunset glow, city lights, mountains, clouds, and other landmarks has been tested, and the results show that birds can be influenced by visible features. This influence is particularly evident in the initial escape movements of newly captured, wild, migratory birds when they are released. However, radar and other methods of observing the natural migratory flight paths have consistently shown that simple escape movements, though important, are not sufficient to account for the migratory behavior of birds, which is undeniably complex and sophisticated.

A great deal of freedom is permissible when considering various theoretical models. But when these models are tested against experimental and observational evidence, the evidence must be taken into account, quoted correctly, and examined thoroughly. Gerrard has scored
poorly on all three points. His use of scientific information is so far from the mark that, at times, his book becomes a work of scientific fiction.

I am compelled to mention one other feature of the book, even though it does not directly relate to the validity of Gerrard’s ideas. He chooses to use insulting and inciting words, presumably in the hope that it will make his readers pay further attention. Instead, many readers will be annoyed by his lack of respect for the human effort and thought that have contributed to establishing our current state of knowledge. Some examples from subject headings: he refers to the founding father of bird orientation research as “Kramer the instigator”; to the first experimental worker on celestial navigation as “Sauer, the planetarium manipulator”; to the massive efforts by Perdeck to capture starlings (Sturnus vulgaris) and displace them laterally during migration as “Perdeck the deporter.” The second section of the book is entitled “Bird Navigation—the Sterile Controversy.” The advertising brochure implies that previous scientific workers have been wasting taxpayers’ dollars. It would be unfortunate if these false and inflammatory accusations should damage the future of a scientific field as productive and as vast as that of animal navigation. The true waste that I see is that Gerrard has failed to read and absorb the massive and exciting literature of bird navigation.

In summary, Gerrard makes some positive suggestions about simple navigation mechanisms; but he makes far more negative and incorrect inferences about past scientific work. On balance, the book does more harm than good.—MELVIN L. KREITHEN.

BIRD MIGRATION IN AFRICA. By Kai Curry-Lindahl. Academic Press, London and New York. 1981, 2 Vols. Vol. 1, xxiii + 444 pp., 255 maps, 7 tables. $85.00. Vol. 2, xxiii + 251 pp., 8 tables, 32 plates (monochrome habitat photographs). $45.50.—The first reaction most of us have had to this pair of books is “Are they worth the price?” The answer, unfortunately, is no. One volume costing $50 would have sufficed rather than two costing a gouging $130. The maps could have been reduced to three per page and more lines added to the average page. The tables that comprise most of the first volume flaunt wasted space, and the text is rambling and redundant. Most disturbing is the duplication of 65 pages of preface materials and the taxonomic and subject indices in both volumes. The editors seem to have consciously expanded this into an expensive book.

The content per se has some strengths and some weaknesses. Bird migration in Africa is an extraordinary subject, both in its biological dimensions and in the well-developed study of it. Would that we had half as much information on Neotropical migrants. The strengths of this book lie in its coverage of the literature of the 1970’s, in the summaries of interesting records of migrant birds on the African continent, and in Curry-Lindahl’s extensive experience with African birds. Many of the interesting observations of migrants reported here are from his own field notes. Valuable also are his views of bird conservation problems, his greatest interest and expertise.

Curry-Lindahl’s text is similar to Moreau’s (1972) The Palearctic-African Bird Migration Systems. His discussions, however, lack Moreau’s depth and do not cut any new intellectual ground. The book thus suffers in comparison to Moreau’s; Moreau set high standards and was able to ask and explore fundamental questions of great dimension.

Bird Migration in Africa does complement Moreau’s (1972) work, which was concerned only with land migrants into Africa from Eurasia. This book devotes considerable space (literally) to other external visitors, including vagrant seabirds and, more importantly, to intra-African migrants. It provides a wealth of details that would have fascinated Moreau,
In conclusion, you should not buy this book if you want to learn more about the phenomenon of migration. If you are working with African birds and must find out what is known about Temminck’s Stints (Calidris temminckii) on their wintering grounds, for example, these volumes will be valuable. But before you commit the funds required, we suggest you look carefully at someone else’s copy to decide whether you really need it for your own library.—Frank B. Gill and A. D. Forbes-Watson.

A COMPARATIVE STUDY OF THE APPENDICULAR MUSCULATURE OF PENGUINS (AVES: SPHENISCIFORMES). By Donald O. Schreiweis. Smithsonian Contributions to Zoology, No. 341. Smithsonian Institution Press, Washington, D.C., 1982:iii + 42 pp., 19 black-and-white figs. Price not given.—In this important study the forelimb and hindlimb muscles are described in detail from dissections of 28 specimens representing six genera and 14 species of penguins. The musculature is illustrated with careful line drawings of a representative species, Eudyptes pachyrhynchus, and both inter- and intraspecific variations are noted in the text. The modification of the forelimbs as flippers for underwater “flight” has had profound effects on the penguin wing. Most of these might once have been termed “degenerative,” but are better regarded as functionally significant simplifications. A dozen muscles have been lost entirely (except for occasional vestiges), while others are small and weak. Eight muscles have lost their contractile tissue and are represented merely by tendons. These changes occur mainly distal to the shoulder, with only nine muscles retaining fleshy fibers. All of this is associated with the flattening of the wing, loss of the alula, and suppression of intramembryonic mobility. There is no patagium as in flying birds, but the propatagialis muscle, which supports that membrane when present, has not been lost; instead its long tendon is attached to the cranial border of the humerus and radius. The pectoral muscles are well developed in association with their propulsive role. The wing elevator, M. supracoracoideus, is unusually large relative to the wing depressor, M. pectoralis. This is related to the fact that penguins achieve propulsion on both the upstroke and downstroke, rather than on the latter alone as in most forms of aerial flight. More discussion or speculation on the functional adaptations of the forelimb musculature would have been welcome. As might be expected, the hindlimb muscles are less distinctively specialized than those of the forelimb. Penguins are unusual in their upright posture, however, but Schreiweis does not comment on possible functional correlations with this habit.

A numerical analysis was carried out, and along with geographical considerations, was used in constructing a tentative phylogeny of the penguins. As is characteristic of such methods, there is no indication of which characters define the various clusters. The phylogeny is similar to one developed earlier by R. Zusi using osteology, and since a phylogenetic diagram is provided it will serve as a hypothesis amenable to testing against the results of future investigations. This work is an important contribution to our knowledge of avian anatomy, and will also be of interest to students of adaptation and evolution.—Robert J. Raikow.

The Birdwatcher’s Dictionary. By Peter Weaver, drawings by Michael Hodgson. T. & A. D. Poyser, Calton, Staffordshire, England. Distributed in USA by Buteo Books, Vermillion, South Dakota; 1981:155 pp., $17.50.—This small volume provides terse definitions for more than 1100 words encountered in the birding world. It is heavily slanted toward a British audience (as expected) so many of the terms (e.g., jizz, carr, skerry, roding) are rarely
heard in the United States. For words that have very simple meanings (e.g., iris, outer tail feather, brood) the definitions in this book may be adequate. However, the definitions of words having more complex meanings are often so short as to be uninformative, misleading or even incorrect. Species, for example, is defined as “a population whose members breed among themselves but not (normally) with members of other similarly defined populations.” Equating species with population is not the usual definition. A speculum is merely “a patch of color on the wing of a duck contrasting with that of the rest of the wing.” No mention is made of the secondaries, so perhaps the blue patch on the Blue-winged Teal would qualify? The standard error (of the mean) is defined as “the difference between an observed mean and the true mean.” If this were the case, the standard error (of the mean) could be reported only if the true mean were known, a rather unlikely condition. I could pick on letters other than “s” but my point should be clear. The meanings of many of the words listed in this book have been seriously compromised for the sake of brevity. I could perhaps recommend this book to readers interested in understanding a little of the British birding slang but there are far too many errors, aside from the inaccuracies, in the words with which I am familiar for me to trust even the simple definitions of those words new to me.—D. Scott Wood.

Waterfowl Ecology and Management: Selected Readings. Compiled by John T. Ratti, Lester D. Flake, and W. Alan Wentz. The Wildlife Society, Inc., Bethesda, Maryland, 1982:xvi + 1328 pp., 19 black-and-white illustrations by Dean Rocky Barrick. $20.00.—This volume contains 125 papers which were previously published in 39 sources. The papers are organized under eight major sections: Historical (4 papers), Reproductive Ecology (38 papers), Population Influences and Characteristics (34 papers), Food Habits and Feeding Ecology (10 papers), Management and Economics (17 papers), Movement and Migration (6 papers), Wintering Waterfowl (6 papers), and Evolution, Hybridization, and Speciation (9 papers). Several of the larger sections are divided into subsections, e.g., Population Influences and Characteristics: Hunting, Population Ecology, Sex Ratios, Disease and Environmental Contaminants, Physiology and Energetics. Sections and subsections are followed by “selected bibliographies,” most of which contain 25+ references; I suspect that many of these are papers that the compilers wished could also have been reprinted in the book. The apparently uneven coverage of major topics largely reflects the historical emphasis of waterfowl research on certain topics, e.g., breeding ecology and food habits, and the lack of research on other topics, e.g., winter ecology. The book is up to date; several of the papers were published since 1980. Although some of the “old” classics are there, e.g., Hochbaum’s (1946) “Recovery potentials in North American waterfowl,” 70% of the papers were published since 1970.

Ratti, Flake, and Wentz state, in the Preface, that “Our primary objective was to compile a comprehensive group of readings suitable as an academic textbook and as a professional reference book.” I think that they have succeeded admirably in that objective as the book certainly contains many of the significant papers on waterfowl. Ted Bookhout says in the Forward, “If six other groups of three compilers drew up their lists of what ought to be included in a book of this type, one could predict six different lists.” But, I expect that any papers on those lists, which are not reprinted in this volume, are listed in the “selected bibliographies.” For example, my list would have contained John Ryder’s (Wilson Bull. 82: 5–13, 1970) paper on the evolution of clutch-size in geese; it is not reprinted in the book, but, sure enough, it is in the bibliography following the section on Evolution, Hybridization, and Speciation. Furthermore, because all the reprinted papers have their original Literature Cited sections, it is likely that any pre-1980 publication about North American waterfowl is
mentioned somewhere in the book. Yes, the book has been, with a few exceptions, restricted to papers about waterfowl research in Canada and the United States. The compilers did this "to restrict the overall length of the book." I suspect that Hugh Boyd, for one, will consider this a serious deficiency, but . . . a 2656 page book?—Dave Ankney.

Die Vogelarten der Erde: Ein Systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen. By Hans E. Wolters. Paul Parey Scientific Publishers, New York, New York, 1982:xx + 745 pp. $210.00.—As the title states, this is a list of the bird species of the world, together with their geographic distributions, and their German and English common names. The indented table of contents sets out Wolters' higher-level classification, which differs in many ways from those familiar to most American readers. It is much more highly "split" at every level; such families as the Pteroedidae, Phoenicopteridae, Musophagidae, and Opisthocomidae, to name a few, have orders to themselves, so the classification has many more orders than usually expected. The same thing is true at the familial and generic levels, e.g., five genera of pittas are recognized instead of the more usual single genus. Wolters advocates cladistic classification and provides a dichotomously branching dendrogram showing hypothetical phylogenetic relationships among his 50 orders. Because there is no character list, however, the basis for this arrangement is not provided.

It is not always easy to find the group that you want. The table of contents goes down to subfamily, but to use it quickly you must be familiar with Wolters' classification, which as noted above, differs greatly from most others. In addition, however, there are alphabetical indexes to scientific names (generic and specific), and to German and English common names.

The bulk of the book consists of the species lists. For each species there is a scientific name (including author and date), German and English common names, and geographic distribution. The latter is in German only, but most of the names are similar to English spelling so those who do not read German should have little trouble with most of them. Subspecies are listed, but separate distributions are not given for them, only the overall distribution of the species. The Peters Checklist is still necessary for details of occurrence.

No, the price of this book is not misprinted above, it really does sell for two hundred ten dollars. There is nothing in its physical nature to give it a retail value more than one-fourth the list price even by current inflated standards. Neither the undoubtedly great efforts of the author nor the limited sales potential can justify a price that makes the book virtually unpurchasable by private individuals. The advertising brochure admits that people cannot afford this book and suggests that you ask your library to buy it. I suggest the opposite. There are other works that cover similar ground at a fraction of the price, and even if there were not, few institutions could withstand many such attacks on their budget. Let us hope that the present case is a publisher's miscalculation; if it is an omen of future trends then technical books as we know them are on the verge of extinction.—Robert J. Raikow.

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Nightingale Wrens of the genus *Microcerculus*: *M. luscinia* (left) and *M. philomela* (right); adults above, juveniles below. From a watercolor painting by Lawrence B. McQueen.
The genus Microcerculus comprises several species of rather small, stub-tailed, highly terrestrial wrens, denizens of humid tropical and subtropical forest understory. Due to their dense habitat and small size they are seldom observed; were it not for the striking songs of the males (whence their vernacular name of "nightingale" wrens) these birds would often escape notice entirely. It is thus not surprising that there are rather few specimens of these inconspicuous birds in museum collections. This, plus the fact that they have the most complex and variable plumages in the Troglodytidae, have made the nightingale wrens the source of numerous taxonomic problems over the years. In their checkered taxonomic history the nightingale wrens of Central America have been considered to comprise from 1–4 species. For nearly half a century only a single species and subspecies has been recognized in this area (Griscom 1932, Hellmayr 1934, Paynter 1960). However, Slud (1958) called attention to the existence of two very distinct and apparently allopatric song types in Costa Rica, one in the north and the other in the southern part of the country. Although he discoursed at length upon the possible taxonomic implications of divergences in song versus morphology in closely related populations, Slud (1958) never attempted to determine if his song types were in fact morphologically distinct. The present study was undertaken to determine whether two distinct morphological types of Microcerculus occur in Costa Rica, and if so whether their distributions coincide with those of the two song types. In the course of this work I have made field observations of the plumage of singing birds, and examined specimens in most major museums. From these studies I conclude that there are two essentially allopatric species of Microcerculus wrens in Costa Rica, which differ strikingly in song and
adult plumage, but are often confusingly similar in their variable immature stages.

NOMENCLATURAL HISTORY

In 1861 Salvin described Microcerculus philomela, designating as the type an unsexed bird from Vera Paz, Guatemala. Five years later he described M. luscinia from two specimens taken at Santa Fé and Santiago, Veraguas, Panamá. In 1888–1889, Ridgway described two additional forms from southern Costa Rica: daulias from Talamanca and orpheus from Pacuare. The two types were fairly similar in plumage, and evidently Ridgway considered them distinct because he thought that Pacuare was on the Pacific slope, rather than the Atlantic. Realizing his error, he synonymized orpheus in 1904 (for original descriptions of these forms see citations in Ridgway 1904); however, he continued to recognize daulias (now including orpheus) as distinct from philomela and luscinia. However, soon thereafter Bangs (1909) lumped daulias into luscinia; he also assigned several recently-taken Underwood skins from northern Costa Rica to luscinia, perhaps because of the apparent distributional gap between philomela (Guatemala-Chiapas) and the Costa Rican-Panamá birds. Noting the presence of similar plumage types in both populations, he suggested that there might be only one species of Microcerculus, M. philomela, in Central America, a suggestion enthusiastically accepted by Carriker (1910).

In the next 20 years enough specimens accumulated to show that nightingale wrens were fairly continuously distributed through Middle America, and a detailed analysis was attempted by Griscom (1932). Based on a sample of 38 specimens, Griscom concluded that there was only one species (and one subspecies, philomela) in Middle America, as suggested by Bangs (1909). He could see no reliable color characters to separate the Guatemalan philomela from specimens of luscinia from central Panamá. To accommodate the diversity of plumage types in his sample, he devised a hypothetical plumage sequence of four stages from juvenile to “full adult”—certainly the most complex sequence ever proposed for a wren. He further lumped philomela (including luscinia) into the South American M. marginatus, finding that some specimens from eastern Darién showed some resemblances to certain Colombian birds. Soon thereafter, Hellmayr (1934:282–283 [footnotes] expressed agreement with Griscom (1932) regarding the Middle American populations. Until very recently, virtually all works on Middle American birds have listed all Middle American Microcerculus as M. m. philomela. However, following Slud’s (1958) description of the two distinct song types in Costa Rica, some authors have adverted the possibility that two species were involved. Blake (1958) mentioned morphological differences (primarily bill color) between a Chiriqui specimen and a series from Chiapas, but concluded that it was an “unlikely possibility” that two species could be distinguished morphologically. Recent popular treatments (Land 1970, Peterson and Chalif 1973) have suggested that philomela was specifically distinct from birds from southern Costa Rica south, and Davis (1972) actually treated philomela and luscinia as separate species on the basis of song (unfortunately, his plate attributes to philomela the coloration of luscinia, and luscinia the coloration of the white-breasted marginatus of South America). The illustration in Edwards’s (1972) Mexican guide also portrays an adult luscinia. Thus, clarification of the morphological picture should benefit field workers as well as systematists. If the two song-types are morphologically distinct, the northern type would be called philomela; the name luscinia applies to the southern song-type.

METHODS

Although this study consists mainly of a critical analysis of museum specimens, its starting point was provided by direct observations of singing male nightingale wrens. Over the years I was able to observe closely males singing each of the songs described by Slud (1958),
attracting them to within 3–5 m by whistled imitations or playbacks of their songs. The former tactic worked better for the “northern” type of song, but I was unable to imitate the high-pitched southern song well enough to consistently attract the birds. Several of the birds so attracted were also collected and proved to be males; thus, I was able to verify the plumage characteristics of the adult males of the two song types. I should also emphasize that males singing one song-type were never attracted to playbacks or imitations of the other song-type (although my sample size is too limited for statistical analysis). Other field observations that proved helpful included sightings of adults followed by begging fledglings on two occasions at Finca La Selva, where only the northern song-type occurs. Field observations also helped me to fill in the distributional picture presented by Slud (1958).

Starting from my field knowledge of the plumage types of adult males, I began an examination of museum specimens, and quickly found that many females resembled closely their respective adult males and were thus probably adults also: sexual dimorphism was slight at best. The real difficulty came with the large number of birds that were more or less variegated below and thus (by analogy with my observations of known fledglings) immature. As the adult plumage types separated nicely along the same geographical lines as did the song types, I provisionally assumed that the immatures would also, an assumption later substantiated by more detailed plumage examinations and mensural data. For each specimen examined, I measured length of exposed culmen (corrected insofar as possible for distortion of the feathers during preparation), wing chord, and tarsus length. The latter feature proved extremely useful in separating a few doubtful cases. I also include in the mensural samples data from several mist-netted birds, since in no case did their measurements deviate significantly from the means calculated for museum specimens of the same song-type. I concluded that the juvenile plumages are the most heavily variegated in both species, and that a distinctive first basic plumage may also occur, but that both are extremely variable. Because of this variability, young birds of the two forms are sometimes extremely difficult to separate on plumage characters alone; but measurements, confirmed by distribution, permit identification of all specimens seen to date.

**SONG TYPES**

The northern (*philomela*) song consists of a series of pure clear whistles, given at a rate of ca. 2/sec over a period often exceeding 15–30 sec. The individual notes are ca. 0.4 sec in duration, on an even pitch or slurred, and at frequencies of between 3–6 kHz, with or without evident harmonics. Successive notes are usually on different pitches, such that the song “rises and falls in an arresting manner” (Slud 1958); the overall effect is that of a slightly tone-deaf person whistling a hymn tune. This song is introduced by a short motif of more rapid (ca. 4/sec) slurred notes, each successive one slightly higher in pitch, but all being close to 4 kHz in frequency.

The southern (*luscinia*) song is extremely different, following an opening motif somewhat resembling that of *philomela*. The song proceeds as a series of long-drawn (ca. 0.8 sec), clear piercing whistles that become successively lower in pitch (ca. 7 kHz at start, to ca. 5.5 kHz at the end of the song). The intervals between successive whistles increase from ca. 2 sec at the start to 5–10 sec at the end. The entire song typically lasts 2–4 min. Sonagrams of these two song types became available too late to be included here, but will be published in the near future.
Within the *philomela* song-type, at least, pronounced local song dialects exist. This dialect is among the most "tuneful"; in other dialects the rhythm may be slightly more choppy, the song itself less strikingly melodious. However, the differences between dialects are far less pronounced than the orders-of-magnitude differences in tempo between the two song types: there is never the slightest question as to which song-type any given song pertains. Moreover, in any given locality all the birds seem to sing the same song; at least, I have never heard more than one song per locality. This is in contrast to the situation in many other wrens, in which several to many song types exist in any given local population, and individual birds often include several song types in their repertories (e.g., Kroodsma 1980). On several occasions I have played back or imitated the northern song in the presence of birds singing *luscinia*-type songs, without ever observing any overt response. On the other hand, males singing *philomela*-type songs often respond strongly by answering and approaching, when I imitate a different local *philomela* dialect in their presence (e.g., birds at Carrillo and Volcán Orozí responded vigorously to my imitation of the La Selva dialect).

**PLUMAGE TYPES**

*Northern song-type* (*M. philomela*).—From field observations I had determined that adult males of this form were rich brown above, scalloped with blackish, and dull grey below, heavily and indistinctly scaled with blackish; juvenals were strongly variegated with pale grey and blackish below, rather more heavily marked above than adults. Examination of museum skins leads me to propose the following plumages:

1. **Definitive (Basic):** Underparts dull dark grey, heavily scaled with dusky to brownish-black, the scaling most distinct and clear-cut on throat (averages decidedly heavier in males), broadest and most indistinct on chest (which may appear nearly solid blackish). Flanks and abdomen dark brown, more or less scalloped fuscous-black. Upperparts rich dark brown, scalloped with black, most closely on crown. Remiges fuscous broadly edged rich brown; wing coverts fuscous-brown, the greater coverts with subterminal bright brown bar, bordered by dusky; this bar becomes paler towards shaft of feather, where a distinct buffy or whitish dot is usually present, giving appearance of a "wingbar" of pale dots; rectrices blackish brown. Iris dark brown; bill black shading to dark horn color on gonys; tarsi blackish.

2. **Juvenal:** More contrastingly marked above and below. Upperparts with dark scaling heavier and often less distinct, or set off by paler subterminal areas near the shafts of the dorsal feathers. Wing pattern like adult but pale spots on greater coverts often whiter and more distinct.
Below dusky blackish, more or less heavily scaled with whitish to pale grey (most heavily marked on throat, which may appear mostly whitish). The pale scaling is in the form of subterminal bars of varying width on otherwise dark feathers (though these often have slate-grey bases). Especially in females, this scaling may be broken up to a greater or lesser extent producing a mottled effect of whitish, grey, and dusky. Abdomen and flanks dark brown, scaled blackish and (faintly) whitish. Bill mostly black, gonys often strongly marked with pale horn color.

(3) Immature (First Basic?): In general resembling definitive basic but scaling of underparts more distinct, especially on lower breast and belly; grey paler, more contrasting with blackish. Dark scaling on breast less heavy, appearing distinctly scaled rather than mostly blackish. Evidently males may sing and breed in this plumage.

Southern song-type (M. luscinta).—From field observations I had concluded that adult males of this song-type were plain brown above with whitish throats and slaty underparts, with at most some brownish or dusky freckling or smudging on the lower breast and belly. Inspection of museum skins allowed me to specify the following plumages:

(1) Definitive (Basic): Throat whitish to (some males) very pale grey, unmarked or the feathers with pale grey bases; breast and belly dull slate, the feathers of the lower breast and belly often tipped or freckled with dull brown. Flanks, abdomen rich dark brown, faintly barred with dusky. Upperparts rich chestnut-brown, mostly immaculate though often lightly scaled dusky on crown. Remiges fuscous-black, broadly margined rich brown; wing coverts fuscous-brown, with a paler, brighter subterminal bar (paler near shaft, but never coalescing into a distinct spot). Iris dark brown; bill black becoming pale to dark horn on gonys; tarsi blackish.

(2) Juvenal: Throat whitish, lightly scaled dusky (especially in males); chest slate-grey, scaled with dark brown and (usually) pale grey, the latter often as a subterminal bar bordered by dusky, base of feather slate; sometimes underparts variegated with all three colors, but with slate-grey predominating on chest; dark bars sometimes broken into spots, giving a "grainy" texture to pattern. Flanks dark rich brown scaled blackish. Upperparts rich dark chestnut-brown scaled with blackish, usually heavily on crown and lightly on back. Wing-coverts patterned as adult but subterminal bar of greater coverts usually strongly paler, even buffy towards shaft, but rarely forming a distinct spot. Mandible mostly horn color, dark towards tip.

(3) Immature (First Basic?): More or less intermediate between juvenal and definitive plumages, more similar to the latter. Throat whitish to pale grey, lightly scaled dusky (more pronounced in males). Chest slate-grey, the feathers with smudgy or mottled brown tips (often more pronounced
in males); lower breast, belly more distinctly scaled with pale grey and dusky, the latter markings often broken and "grainy." Above with scaling on back usually faint to obsolete.

From the foregoing it should be evident that the adults of the two song-types are quite distinct in plumage. In both forms the general tendency is from a more contrastingly marked juvenile plumage to a more uniformly marked or immaculate, less contrasty adult plumage. The great variability in young birds definitely complicates things; in particular, some juvenile southern birds may resemble "first-basic" northern types. Certainly the proposed plumage sequences should be taken as hypothetical at this stage, in the absence of data on skull ossification, returns of banded birds, etc. However, I feel that at least the general direction of change is correct, and the sequences themselves are much more in accord with what is known in the Troglodytidae (see Ridgway 1904) than, for instance, the incredibly complex system of Griscom (1932). The starting point of this Procrustean bed (into which two quite different sequences were forced), was the erroneous assumption that all heavily-scaled birds were immature. Thus, the adult of the northern song-type (dark in color, heavily scaled) was assumed to be the juvenile plumage, the adult of the southern form (pale in color, little or no scaling) the adult, with the various immature forms (dark and light scaling or variegation) constituting several intermediate stages. Griscom (1932) stated that he had representatives of all of his plumage types from throughout the range of the "species"; having examined all the material available to Griscom plus many more recently taken specimens, I can state categorically that this is not the case. The problems lie in the confusing similarity of the immature plumages of *luscinia* and *philomela*, and in the fact that Griscom's knowledge of distributions of these wrens was understandably incomplete due to the inadequate material available.

MEASUREMENTS

Correlated with differences in plumage between the song-types are differences in measurements (Table 1). In general, the southern song-type (*luscinia*) is the larger bird, sex for sex, being particularly significant in the case of tarsal length (Table 2). Males average larger than females in all dimensions, and this difference is most marked in southern birds. However, because of the possibility of missexed specimens I do not care to push this comparison too far. Nevertheless, tarsal length alone suffices to separate over 80% of all specimens, regardless of sex; those with tarsi below 21 mm are nearly all *philomela*; birds with tarsi over 21.5 mm are nearly all *luscinia*. Using all three measurements at least 90–95% of all specimens can be identified to song-type.
Table 1
Measurements (mm) of Nightingale Wrens (Microcerculus) from Central America

<table>
<thead>
<tr>
<th>Form</th>
<th>Sex</th>
<th>N</th>
<th>$\bar{x} \pm SD$</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Exposed Culmen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>philomela</td>
<td>♂️</td>
<td>31</td>
<td>16.93 ± 0.54</td>
<td>15.9–18.2</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>21</td>
<td>16.86 ± 0.56</td>
<td>16.0–18.1</td>
</tr>
<tr>
<td>luscinia</td>
<td>♂️</td>
<td>27</td>
<td>18.27 ± 0.77</td>
<td>16.9–20.0</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>24</td>
<td>17.89 ± 0.89</td>
<td>15.9–19.4</td>
</tr>
<tr>
<td>B. Wing Chord</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>philomela</td>
<td>♂️</td>
<td>31</td>
<td>55.25 ± 1.24</td>
<td>52.4–58.6</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>19</td>
<td>54.41 ± 1.80</td>
<td>51.7–58.3</td>
</tr>
<tr>
<td>luscinia</td>
<td>♂️</td>
<td>27</td>
<td>57.30 ± 1.93</td>
<td>53.4–62.3</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>23</td>
<td>55.32 ± 1.66</td>
<td>52.5–59.2</td>
</tr>
<tr>
<td>C. Tarsus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>philomela</td>
<td>♂️</td>
<td>31</td>
<td>20.76 ± 0.41</td>
<td>19.9–21.5</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>19</td>
<td>20.63 ± 0.52</td>
<td>19.8–21.6</td>
</tr>
<tr>
<td>luscinia</td>
<td>♂️</td>
<td>27</td>
<td>22.59 ± 0.74</td>
<td>21.3–23.7</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>24</td>
<td>21.92 ± 0.64</td>
<td>20.6–23.3</td>
</tr>
<tr>
<td>D. Weight (g)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>philomela</td>
<td>♂️</td>
<td>7</td>
<td>18.64 ± 1.58</td>
<td>17.4–21.5</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>4</td>
<td>17.02 ± 0.47</td>
<td>16.4–17.4</td>
</tr>
<tr>
<td>luscinia</td>
<td>♂️</td>
<td>5</td>
<td>20.08 ± 1.42</td>
<td>18.2–22.0</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>4</td>
<td>17.45 ± 0.48</td>
<td>17.0–18.0</td>
</tr>
</tbody>
</table>

Geographic variation within and between song-types is evaluated in Table 3. In general, significant geographical variation within song-types is lacking, but comparisons between Costa Rican populations of the two yield highly significant differences (all measurements of males, and tarsal length in females). In general, the smaller degree of difference between females of the two song-types reflects the much smaller degree of sexual dimorphism in philomela, compared to luscinia (cf. Table 2). Indeed, the only geographical comparison among females to yield a significant difference was between the two song-types in Costa Rica with respect to tarsus length. In other measurements female luscinia were larger than those of philomela in Costa Rica; only in bill length were Costa Rican females notably larger than those of more northern populations of philomela. (However, note that such geographical comparisons are hindered by the extremely small Honduras-Nicaragua sample.) In both wing and tarsus, Costa Rican populations of the two song-types are at least as different (and usually more so) as are more allopatric populations. The only within-song-type
Table 2

Statistical Comparisons (Student’s t) Between Mean Measurements of Different Forms of Nightingale-Wren, and Between Sexes of Each Form (all specimens combined)

<table>
<thead>
<tr>
<th></th>
<th>Exposed culmen</th>
<th>Wing chord</th>
<th>Tarsus</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta$ luscinia vs $\delta$ philomela</td>
<td>7.79***</td>
<td>4.76**</td>
<td>13.56***</td>
</tr>
<tr>
<td>$\Phi$ luscinia vs $\Phi$ philomela</td>
<td>4.53**</td>
<td>1.69</td>
<td>6.97***</td>
</tr>
<tr>
<td>$\delta$ vs $\Phi$ philomela</td>
<td>0.78</td>
<td>1.34</td>
<td>0.09</td>
</tr>
<tr>
<td>$\delta$ vs $\delta$ luscinia</td>
<td>3.92**</td>
<td>1.49</td>
<td>4.09**</td>
</tr>
</tbody>
</table>

$^* = P < 0.05, ~ ^{**} = P < 0.01, ~ ^{***} = P < 0.001.$

comparison to yield a significant difference was tarsus length between the two Panamá samples of male luscinia. Males from central and western Panamá tend to have shorter tarsi than do those of either Costa Rica or eastern Panamá (the same is true of females, but the differences are not significant). Only in bill length might there be reason to suspect a clinal change over all populations (with culmen length increasing from north to south), but even here the cline is decidedly ‘stepped’ between the two song-types in Costa Rica (especially in males). Within Costa Rica I can discern no geographical trends in measurements, but sample sizes from particular areas are too small to permit meaningful statistical analyses. Suffice it to say that the most nearly sympatric populations of the two song-types seem to differ by about as much as do more allopatric populations.

**DISTRIBUTION**

The known distributions of northern and southern song- and plumage-types in Costa Rica are mapped in Fig. 1. As can be seen, distribution of song-types (based on my field observations and data in Slud [1958]) and plumage types (based on specimens) coincide precisely: there is no question that Slud’s (1958) song-types are also morphological entities—two kinds of nightingale wren occur in Costa Rica. Their distributions are essentially allopatric, and with the data now in hand it is possible to specify distributional limits in greater detail than did Slud (1958).

The northern bird, philomela, is most abundant in the foothills and adjacent lowlands of the northern half of the Atlantic slope. On the Pacific side it does not occur in lowland Guanacaste, but only in humid-forested ravines along the bases of the Guanacaste volcanos. It is, in my experience, most characteristic of ravines in hilly, forested country; the bird I heard at Tortuguero was not in lowland swamp forest but on the slopes of
a low range of hills ca. 5 km inland from the coast. Its southern limit is
the northeastern edge of the Cordillera Central near the town of Guácimo;
it ranges north to Chiapas, México. Its upper elevation limit is around
1400 m, but it is not common much above 1000 m in most areas.

The southern bird, *luscinia*, is associated in Costa Rica with the foothills
of the Cordillera de Talamanca and the adjacent lowlands. On the Pacific
slope of Costa Rica, it ranges north to the hills south and west of the
Meseta Central (the south side of the Río Barranca watershed [P. Slud,
in litt.]); on the Atlantic slope, to about the northern edge of the watershed
of the Río Reventazón. In the Pacific lowlands, its northward distribution
is probably limited by the drier conditions north of the mouth of the Golfo
de Nicoya; it is also not known from the Meseta Central, which again is
somewhat drier than the surrounding hills. Southwards, *luscinia* ranges
to eastern Darién, Panamá. In my experience the habitat of *luscinia* is
quite similar to that of *philomela*, but it seems perhaps less limited to
hilly country, and may be found in old second growth as well as forest (cf.
Slud 1964). It occurs from near sea level to about 1200–1400 m on the
Atlantic slope, and up to ca. 1700 m locally in the somewhat more seasonal
forests on the Pacific slope of the Cordillera de Talamanca.

The ranges of the two forms of *Microcerculus* approach one another
closely on both slopes of Costa Rica, but the nature of the contact zone
(if any) is difficult to discern at present, perhaps largely due to the severe
habitat disturbance in the critical areas. On the Pacific side, the Río Bar-
ranca watershed is mostly deforested, and the remnant patches of forest
are probably too small and isolated to support viable *Microcerculus*
populations. On the Atlantic slope, severe habitat disturbance in the Reven-
tazón drainage dates back over a century. There may be a zone on the
northeastern edge of the Cordillera Central where neither species occurs
at present. At any rate, I failed to find any *Microcerculus* in remnant forest
patches between Siquirres and Guácimo on trips in 1975 and 1979. Prior
to habitat disturbance, I suspect that the contact between the two forms
was always abrupt, with complete replacement of one form by the other
within a short distance, perhaps reflecting competitive exclusion, given
their similar ecology and morphology (cf. Diamond 1980). Moreover, I
suspect that the sharp dividing line between the two might have been
maintained by interspecific territoriality. The similarity of the opening
motifs of the songs of the two forms is interesting in this connection. One
could hypothesize that it might permit birds of one form to recognize those
of the other form as potential territorial rivals, while the rest of the song
might help to maintain reproductive isolation, as evidently occurs in meadow-
owlarks (*Sturnella* spp.) (Szijj 1966).

It is interesting that the dividing line between the two forms falls in or
Table 3

Geographic Variation in Measurements* of Microcerculus Wrens of Middle America. Mean Measurements for Different Geographical Areas (Guatemala-Chiapas, Honduras-Nicaragua, Costa Rica, Western and Central Panamá, Eastern Panamá) are Compared by t-tests.

<table>
<thead>
<tr>
<th>Sex, Taxon</th>
<th>Area</th>
<th>Bill Measurement</th>
<th>Wing Measurement</th>
<th>Tarsus Measurement</th>
</tr>
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<tr>
<td></td>
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<tr>
<td>Males</td>
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<td></td>
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</tr>
<tr>
<td>philomela</td>
<td>Guat.-Chis.</td>
<td>16.82 ± 0.46</td>
<td>55.18 ± 1.30</td>
<td>20.69 ± 0.38</td>
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<td></td>
<td>(12)</td>
<td></td>
<td>(12)</td>
<td>(12)</td>
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<tr>
<td></td>
<td>Hond.-Nica.</td>
<td>16.80 ± 0.67</td>
<td>55.65 ± 0.76</td>
<td>20.98 ± 0.37</td>
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<td></td>
<td>(7)</td>
<td>0.03</td>
<td>0.87</td>
<td>1.66</td>
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<tr>
<td></td>
<td>C. Rica</td>
<td>17.12 ± 0.64</td>
<td>55.10 ± 1.16</td>
<td>20.68 ± 0.44</td>
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<td></td>
<td>(13)</td>
<td>0.99</td>
<td>1.20</td>
<td>1.65</td>
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<tr>
<td></td>
<td>C. Rica</td>
<td>18.01 ± 0.51</td>
<td>57.25 ± 1.68</td>
<td>22.52 ± 0.80</td>
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<td>(11)</td>
<td>3.88**</td>
<td>3.95**</td>
<td>7.59***</td>
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<td></td>
<td>W. + C. Pan.</td>
<td>18.29 ± 1.04</td>
<td>56.25 ± 1.64</td>
<td>22.11 ± 0.66</td>
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<td></td>
<td>(7)</td>
<td>0.76</td>
<td>1.29</td>
<td>1.23</td>
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<td>E. Pan.</td>
<td>18.62 ± 0.68</td>
<td>58.16 ± 2.19</td>
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<td>0.78</td>
<td>1.91</td>
<td>3.19**</td>
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<td>Females</td>
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<td>Guat.-Chis.</td>
<td>16.73 ± 0.30</td>
<td>54.33 ± 1.68</td>
<td>20.64 ± 0.41</td>
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<td>(11)</td>
<td></td>
<td>(11)</td>
<td>(11)</td>
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<tr>
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<td>Hond.-Nica.</td>
<td>16.40</td>
<td>54.50 ± 1.97</td>
<td>21.00 ± 0.28</td>
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### TABLE 3
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<th>Area</th>
<th>Bill Measurement</th>
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<th>Wing Measurement</th>
<th>t</th>
<th>Tarsus Measurement</th>
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<td>17.07 ± 0.74</td>
<td>1.73</td>
<td>54.35 ± 1.93</td>
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<td>20.65 ± 0.69</td>
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<td>17.74 ± 0.86</td>
<td>1.64</td>
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<td>22.14 ± 0.54</td>
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<td>(6)</td>
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<td>17.74 ± 1.04</td>
<td>0.02</td>
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<td>0.16</td>
<td>21.66 ± 0.75</td>
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<tr>
<td>W. + C. Pan.</td>
<td></td>
<td>18.16 ± 0.64</td>
<td>0.96</td>
<td>54.75 ± 1.56</td>
<td>1.48</td>
<td>22.03 ± 0.51</td>
<td>1.29</td>
</tr>
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<td>(10)</td>
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</tr>
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</table>

* Measurements given are means, SD, and N.

* *P < 0.05, ** *P < 0.01, *** *P < 0.001.
Fig. 1. Distribution of two forms of *Microcerculus* in Costa Rica. Circles = *M. philomela* (northern song-type); triangles = *M. luscinia* (southern song-type); locality records based on song (open figures), specimens (half-solid figures), or both (solid figures). R = Río Reventazón.

near the Reventazón drainage, as this area is evidently a zone of considerable floral and faunal turnover (Stiles 1979). Among the bird species reaching their northern or southern limits in this area are Blue-headed Parrot (*Pionus menstruus*), Sulphur-rumped Tanager (*Heterospingus rubrifrons*), Coppery-headed Emerald (*Elvira cupreiceps*), and *Microcerculus* spp. (cf. Slud 1958, 1964). In plants, several different taxa of *Heliconia* meet and hybridize in this area (Stiles 1979), and considerable turnover occurs in several other groups as well (J. Gómez Laurito, pers. comm.).
Considerable species turnover also occurs here in butterflies (P. J. De Vries, pers. comm.).

The geological and historical reasons for this degree of turnover in this area are obscure. One possibility is that the different forms have spread from different Pleistocene wet-forest refugia, although the exact locations for these are still somewhat conjectural (cf. Muller 1973, Haffer 1974). The Cordillera Central and the Cordillera de Talamanca are roughly the same age (early Pleistocene) in their present forms (Lloyd 1963), but even small differences in the timing of their respective uplivings might have had major effects on their respective biotas. In any case, historical factors must be implicated in trying to explain the degree to which 'suture zones' in so many animal and plant groups coincide in an area of such essentially uniform climate and vegetation as the Caribbean lowlands of Costa Rica. The fact that the Río Reventazón is the major river draining the area between the two cordilleras suggests that the latter must have had a major effect, perhaps in producing the weather patterns responsible for Pleistocene refugia.

CONCLUSIONS

Based upon song type, morphology, and distribution, I have no hesitation in calling the two Microcerculus wrens of Costa Rica distinct species. I have never seen an adult specimen that I could confidently call a hybrid, nor have I ever heard an intermediate song. At present I know of no area where the two forms are sympatric, though an exhaustive survey of the area around the Reventazón drainage might be enlightening in this respect. The similarity in immature plumages and the difficulty of identifying young birds by plumage alone is neither surprising nor distressing: it is the adult plumages and songs that will function as isolating mechanisms. The northern bird should be called Microcerculus philomela Salvin. Given the irregular or clinal nature of the variation within this form, recognition of subspecies is unwarranted. The exact status of luscinia Salvin is uncertain, for it may be conspecific with one or more members of the South American M. marginatus complex, which, as currently constituted, includes several forms rather different in appearance. Closest geographically to luscinia are the transandean forms taeniatus and squamulatus, with scaly-grey breasts in all plumages; true marginatus occurs east of the Andes and has a plain white breast. Various observers report that birds of these forms from a wide area in northern South America (from Venezuela to Perú) give luscinia-like songs (fide E. Eisenmann, B. Coffey, J. Fitzpatrick, R. Ridgely, P. Schwartz). On the other hand, in Perú there is great variability in song-type, with the song from southern Perú sounding
quite different from either *philomela* or *luscinia* (fide J. Fitzpatrick). All Peruvian birds are currently classified as a single subspecies, *marginatus*; indeed, the situation seems suspiciously reminiscent of that in Middle America, and a great deal of field and museum work will be required to resolve it. For the present, I think it most convenient to emphasize the morphological picture in Central America by considering *luscinia* a species (or semispecies), pending detailed study of South American birds.

With respect to English vernacular names, it is worth noting that "nightingale-wren" was originally applied by Salvin only to *philomela* (which he had doubtless heard in Guatemala), and was later extended to allied forms without benefit of voice data. The song of *luscinia* and its allies in no way resembles that of a nightingale (for that matter, neither does that of *philomela*, except in its possession of strikingly musical quality). Taking voice into account (since the birds are far more often heard than seen), I would recommend that the group name "nightingale-wren" be restricted to *philomela* (which would be called simply Nightingale-Wren). I agree with a suggestion by E. Eisenmann that "whistler-wren" would be an appropriate group name for those birds singing *luscinia*-like songs. If *luscinia* is considered a species or semispecies in its own right, it could be called Northern Whistler-Wren. Should the entire complex be considered as a single species, the unmodified name Whistler-Wren would of course suffice for all.

**SUMMARY**

Evidence from morphology and distribution is combined with data on song to demonstrate the existence of two species of *Microcerculus* wrens in Central America: *M. philomela* Salvin (Nightingale-Wren), ranging from Chiapas, México, to central Costa Rica; and *M. luscinia* Salvin (Northern Whistler-Wren), which ranges from central Costa Rica to eastern Darién, Panamá. The importance of the Reventazón region of the Caribbean slope of Costa Rica as a zone of faunal and floral turnover is indicated. Perhaps because of habitat disturbance and/or ecological incompatibility, there is no known area of sympathy of the two forms at the present time.

**ACKNOWLEDGMENTS**

During this study I have profited greatly from the advice and encouragement of E. Eisenmann, L. F. Kiff, and A. R. Phillips. The fieldwork was made possible by a Chapman-Naumburg Fellowship from the American Museum of Natural History, a grant from CONI- CIT, and funds from the Vicerrectoría de Investigación, Universidad de Costa Rica. Valuable data on nomenclature and on the South American birds were provided by E. Eisenmann; P. Slud provided two unpublished distributional records. N. Flood did the figure. I also thank the curators and staffs of the museums mentioned below for permission to examine specimens in their care, and for many courtesies extended during my often frenetic visits to the Intertropical Zone.

Specimens were examined from the following museums (numbers in parentheses are specimens of *philomela* and *luscinia*, respectively): American Museum of Natural History (8, 14); British Museum (Natural History) (8, 1); Field Museum of Natural History (7, 2); Loui-
siana State University Museum of Natural History (5, 2); Museum of Comparative Zoology (8, 8); Museo Nacional de Costa Rica (0, 2); Museo de Zoología, Universidad de Costa Rica (3, 1); University of Michigan Museum of Zoology (1, 1); U.S. National Museum (1, 17); University of California, Los Angeles (2, 1); Western Foundation of Vertebrate Zoology (4, 1). In addition, data from four philomela and three luscinia, mist-netted, measured, and released, are included.

LITERATURE CITED


ESCUELA DE BIOLOGÍA, UNIVERSIDAD DE COSTA RICA, CIUDAD UNIVERSITARIA, RODRIGO FACIO, COSTA RICA, CENTRAL AMERICA. ACCEPTED 8 APRIL 1982.
THE RELATIONSHIPS AND EVOLUTION OF THE SOUTHWEST PACIFIC WARBLER GENERA 
VITIA AND PSAMATHIA (SYLVIINAE)

RONALD I. ORENSTEIN AND H. DOUGLAS PRATT

The genera Vitia and Psamathia include three species of sylviine warblers of forest undergrowth from Micronesia and Melanesia: the Fiji Warbler (V. ruficapilla) with races on Viti Levu (V. r. badiceps), Vanua Levu (V. r. castaneoptera), Taveuni (V. r. funebris), and Kadavu (V. r. ruficapilla); the Shade Warbler (V. parens), a little-known bird of the mountains of San Cristobal, and probably Bougainville (Hadden 1981), in the Solomon Islands; and the Palau Bush-Warbler (Psamathia annae), restricted to Palau (Mayr 1945). Baker (1951:221) suggested, on the basis of external morphology, that P. annae was allied to Cettia diphone seebohmi of Luzon. Pratt et al. (1980) included the Palau bird in Cettia, and E. Mayr (in litt.) agrees with this treatment. The position of Vitia has been more obscure, although Delacour (1942-43) suggested that it, too, was allied to Cettia. Ramsay (1875), in his description of Vitia, compared V. ruficapilla to Malurus (Malurinae) and Sericornis (Acanthizinae). Finsch (1876) placed V. r. ("Drymochaera") badiceps between Camaroptera and Orthotomus (Sylviinae). Mayr (1936) compared V. parens to Sericornis nouhuysi, but concluded that the two were not related. Morony et al. (1975) list Psamathia after Cettia, but place Vitia near the end of the Sylviinae with other genera of obscure affinity such as Ortygocichla and Megalurulus. This paper presents evidence that Vitia and Psamathia are Pacific island representatives of Cettia, closely related to C. diphone.

METHODS

The authors independently made observations and tape recordings of V. r. badiceps on Viti Levu (Orenstein, June 1974; Pratt, July 1977). Pratt also observed V. r. castaneoptera on Vanua Levu, but his tape recordings of it were lost. Pratt made extensive observations and recordings of Psamathia annae during several visits to Palau (Pratt et al. 1980) and observed an introduced population of the Japanese Bush Warbler (Cettia diphone cantans) on Oahu in the Hawaiian Islands intermittently from 1974-1980. Both authors studied tape recordings of various Cettia species in the collection of the Laboratory of Ornithology, Cornell University. Our own recordings are now archived in that collection. Orenstein examined study skins of Cettia, Vitia, and Psamathia in the American Museum of Natural History and the Museum of Zoology, University of Michigan.

CHARACTER ANALYSIS

Song.—The song of V. r. badiceps is a clear unmodulated whistle, usually interrupted by brief pauses near the beginning, rising gradually in
volume and followed by a loud warble of 2–4 phrases at a generally higher pitch. Single syllables vary considerably within a bout of singing. The whistle may be given at different pitches, and the phrases of the concluding warble may vary both in number and form. The warble may occasionally be uttered without the introductory whistle and vice versa. Figure 1 (a–f) illustrates songs of *V. r. badiceps*. Figure 1 (a–d) represents four consecutive songs of a single individual. The song of *V. r. castaneoptera* is similar in general pattern (Pratt, pers. obs.). Pairs of *V. ruficapilla* may perform duets, the song of one bird (presumably the male) being followed, or occasionally preceded, by a sharp *tsic-tsic* from the other (Watling 1982). The voice of *V. paren* is not definitely known, but Cain and Galbraith (1956:269) heard “a mellow musical whistle . . . *wuwu* and
"weedledele wewi wew" on San Cristobal that was attributed by natives to this species. An unidentified song of pure whistled tones, commonly heard between 850 and 1300 m elev. on Bougainville, may be that of *V. parens* (Hadden 1981).

The primary song of *P. annae* resembles that of *V. ruficapilla* in structure, but differs in phrasing. The whistle is lower in pitch and more often given without the concluding warble (Fig. 1g). Its pitch may slur up or down, and, as in *V. ruficapilla*, may be broken by pauses near the outset. Succeeding whistles usually vary in pitch (Pratt et al. 1980). The warble, when given, may consist of more phrases than that of *V. ruficapilla*, but otherwise closely resembles the warble of the Fiji bird (Fig. 1h–i). A second song, consisting of repetitions of the warbled phrases only, resembles somewhat the "valley-crossing call" (Austin and Kuroda 1953) of *C. d. cantans* (Pratt, pers. obs.) (Fig. 1j).

The genus *Cettia* comprises three subgenera, two of which (*Cettia* and *Urosphena*) do not vocally resemble *Psamathia* and *Vitia*. Songs of Cetti’s Warbler (*C. cetti*), in the monotypic subgenus *Cettia*, contain no long whistles, but are loud and uttered from concealment like those of most of the genus (Bruun and Singer 1970). The song of the Stub-tailed Bush Warbler (*C. [Urosphena] squameiceps*) is a thin, cicada-like series of notes (Dement’ev and Gladkov 1954, Yamashina 1961); that of the Bornean Short-tailed Bush Warbler (*C. [U.] whiteheadi*) a long drawn-out squeak (Smythies 1960); that of the Pale-footed Bush Warbler (*C. [U.] pallidipes*) a loud *rip ... rip-chick-a-chick* (Fleming et al. 1976); while that of the Timor Bush Warbler (*C. [U.] subulata*) is apparently unknown.

Figure 2 illustrates the songs of four species of the third subgenus of *Cettia*, *Horeites*. Except for those of the Gray-sided Bush Warbler (*C. brunnifrons*) (Fig. 2f–g) and Müller’s Bush Warbler (*C. vulcania*), these songs resemble those of *Vitia* and *Psamathia* in being divisible into two parts, the first of which is a clear, unmodulated or slowly modulated whistle or series of whistles. In the extremely drawn-out song of the Yellowish-bellied Bush Warbler (*C. acanthizoides*) the concluding portion is a trill of 10 sec or so duration. The songs of *C. diphone* and the Strong-footed or Brownish-flanked Bush Warbler (*C. fortipes*), however, conclude with a warble closely resembling that of *P. annae* or *V. ruficapilla*. The warble of *C. fortipes*, however, consists of longer, more widely spaced and broadly modulated phrases than those of *C. diphone*, *P. annae* or *V. ruficapilla*, although as the warbles of all four species are highly variable these differences may not be consistent. Figure 2e shows a song of *C. vulcania*, a species recently separated from *C. fortipes* primarily on the basis of its distinctive voice (Wells 1982).
The song of the Chestnut-Crowned Bush Warbler (C. major) has not been described. Tapes were not available for the song of the Aberrant Bush Warbler (C. flavolivacea), described as “a short, very high and thin whistle” by Ali (1977:174). Among the species examined, however, C. fortipes and particularly C. diphone show the closest vocal resemblance to Psamathia and Vitia, indeed resembling these species more than they do other species of Cettia.

Eggs and nests.—Several clutches of eggs of V. r. badiceps have been collected (Nehrkorn 1879, Oates and Reid 1905). The eggs are reddish-chocolate or chocolate in color, and moderately to highly glossy (Oates and Reid 1905). These eggs are, according to Nehrkorn (1879), virtually identical to those of P. annae, C. diphone, and C. cetti. Pratt et al. (1980)
<table>
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<td>3.4 ± 0.014</td>
<td>3.1 ± 0.015</td>
</tr>
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</table>

* Tails exhibiting marked wear were not measured.
* Measurements of culmen (from nostril), bill width, and bill depth were taken at the level of the anterior end of the nasal cavity. (Bill depth was not measured on specimens with improperly occluded bills.)
also describe a dark purplish-brown egg of *P. annae*. Such dark egg colors are unusual among passerines, and egg color has been used as a generic character in *Cettia* (Mayr, in litt.).

*Vitia ruficapilla* builds a “large, rather crude nest . . . domed with the entrance hole above mid-height, on one side” (Watling 1982:108). Nest structure is variable in *Cettia*. *C. f. fortipes* builds nests “varying from a deep cup to a domed or globular structure with a large entrance near the top” (Ali and Ripley 1973:11). Pratt et al. (1980) commented on the similarity of the nest of *P. annae* to the domed nest of *C. d. cantans* described by Austin and Kuroda (1953). The nest of *C. d. borealis* is a deep, symmetrical cup (Dement’ev and Gladkov 1954).

**Morphology.**—*Vitia* and *Psamathia* resemble species of *Cettia*, particularly those in the subgenus *Horeites*, in size, proportions, and plumage pattern (Tables 1, 2; Fig. 3; cf. Delacour [1942–43] for analyses of subgenera). They differ chiefly in having longer bills, a feature common in insular representatives of mainland genera (Grant 1965, Schoener 1965). Within *Cettia*, insular races of *C. diphyne* (*diphyne, restrictus*) have longer bills than the continental (*borealis, sakhalinensis, canturianus*) or mainland Japanese (*cantans*) subspecies (Vaurie 1954, 1959). *Cettia, Vitia,* and *Psamathia* all differ from most sylviine genera in having 10, rather than 12, rectrices (Ali and Ripley 1973; Orenstein, pers. obs.). This distinction also sets these warblers apart from *Sericornis* (Acanthizinae) to which *V. parens* has been compared (Mayr 1936). The rufous to chestnut crown and cinnamon face of *V. parens* and *V. ruficapilla* resemble those of *C. major, C. brunifrons*, and particularly *C. d. seebohmi*.

Among themselves, the two species of *Vitia* and *P. annae* exhibit few divergences. *Vitia parens* differs from *V. ruficapilla* primarily in being browner, with a more extensive cinnamon wash on the cheeks. Means for the three males measured fall within the range of means for races of *V. ruficapilla* for all characters examined except tail length, for which wear may have affected the results (Tables 1, 2). *Psamathia annae* differs from both *Vitia* spp. in lacking rufous or cinnamon in the plumage and in larger size. In these respects the Palau Bush-Warbler closely resembles *C. d. cantans* of Japan.

The juvenile of *V. parens*, known from a unique specimen in the American Museum of Natural History (Mayr 1936), differs markedly from its adult but resembles fairly closely the adult plumage of *P. annae* (Table 2, Fig. 2). It shares with *P. annae*, though not with the adult *V. parens*, a generally olive coloration with a bright olive-yellow throat. Although it differs from the Palau bird in being darker with a blackish crown and brown thighs and flanks, and in lacking a supraciliary stripe, placed between specimens of *V. parens* and *P. annae* it might easily be taken for the young of the latter rather than of the former.
<table>
<thead>
<tr>
<th>Table 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>PLUMAGE CHARACTERISTICS OF <em>CETTIA DIPHONE</em>, <em>PSAMATHIA ANNAE</em>, <em>VITA PARENS</em> AND <em>V. RUFICAPILLA</em></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Crown</th>
<th>Back</th>
<th>Face and cheeks</th>
<th>Underparts</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. d. cantans</em></td>
<td>Olive Green$^a$</td>
<td>Olive Green</td>
<td>Olive Grey</td>
<td>Pale Grey washed with Citrine</td>
</tr>
<tr>
<td><em>C. d. seebohmi</em></td>
<td>Cinnamon Brown (brighter than back)</td>
<td>Cinnamon Brown</td>
<td>Medium Neutral Grey, washed with Cinnamon</td>
<td>Grey, washed with Olive on flanks</td>
</tr>
<tr>
<td><em>P. annae</em></td>
<td>Greyish Olive</td>
<td>Greyish Olive</td>
<td>Olive Yellow, brightest on throat</td>
<td>Olive Yellow</td>
</tr>
<tr>
<td><em>V. pares</em> (juv.)</td>
<td>blackish</td>
<td>dark Greyish Olive</td>
<td>Olive Yellow; center of throat bright Olive Yellow</td>
<td>Olive Yellow; thighs and flanks brown</td>
</tr>
<tr>
<td><em>V. pares</em> (ad.)</td>
<td>Russet</td>
<td>Olive Brown (browner than <em>ruficapilla</em>)</td>
<td>Cinnamon (extends to throat)</td>
<td>Olive washed with Cinnamon</td>
</tr>
<tr>
<td><em>V. r. ruficapilla</em></td>
<td>Cinnamon Rufous</td>
<td>Olive Brown</td>
<td>Cinnamon</td>
<td>Grey washed with Olive on flanks</td>
</tr>
<tr>
<td><em>V. r. badiceps</em></td>
<td>Chestnut</td>
<td>Olive Brown</td>
<td>Medium Neutral Grey, washed with Cinnamon</td>
<td>Grey washed with Olive on belly and flanks</td>
</tr>
<tr>
<td><em>V. r. funebris</em></td>
<td>Russet</td>
<td>Olive Brown (darkest and greyest race)</td>
<td>Cinnamon, mottled with blackish</td>
<td>Grey, washed with Olive on belly and flanks</td>
</tr>
<tr>
<td><em>V. r. castaneoptera</em></td>
<td>Chestnut</td>
<td>Olive Brown (brownest race)</td>
<td>Medium Neutral Grey, washed with Cinnamon</td>
<td>Grey, washed with Olive on flanks</td>
</tr>
</tbody>
</table>

$^a$ Capitalized names of colors from Smithe (1975).
The presence of pure monotonal whistles as song components might be the result of similar selection pressures. The Fiji Warbler, the Shade Warbler, the Palau Bush-Warbler, as well as many bush-warblers of the genus Cettia, are all birds of the lower forest levels. Pure whistles may have selective value related to their carrying ability in the forest understory (Morton 1975), and occur in the songs of understory species of many diverse avian families. Similar whistles occur, for example, in the African sylviine genus Bathmocercus (Chappuis 1980). But the whistle-warble songs of P. annae, V. ruficapilla, C. fortipes, and C. diphyne appear too similar to be the result of simple habitat similarities. All Horeites spp., including those whose songs are not like those of Psamathia and Vitia, are birds of forest understory (Ali and Ripley 1973, King et al. 1975).

Some doubt the utility of egg color in taxonomy (Lack 1958). The unusually dark egg colors of Psamathia, Vitia, and Cettia (Horeites), how-
ever, probably represent a synapomorphy (i.e., a shared derived character).

Rectrix number is not always a valid generic character. The Cinnamon Bracken Warbler (*Bradypterus cinnamomeus*), an African sylviine placed in a genus allied with *Cettia*, may have either 10 or 12 rectrices (Delacour 1942–43). The presence of 10 rectrices, however, as with dark egg color, is sufficiently rare in the Sylviinae to be of significance when it occurs in species that share other apparently derived characters. And while the general similarities of plumage and body proportions cannot carry much taxonomic weight in a group containing as many similar species as do the Sylviinae, they reinforce the conclusion that *Vitia*, *Psamathia*, and *Cettia* are closely related.

On the basis of song structure, egg color, and external morphology, therefore, we believe that *Vitia* and *Psamathia* are best regarded as sharing a common ancestry with *C. diphone* within *Horeites*, and thus undeserving of generic or even subgeneric status. Following this proposal the species *C. annae*, *C. parens*, and *C. ruficapilla*, here listed alphabetically and in order of increasing distance from continental Asia, should be included in the subgenus *Horeites* following *C. diphone*. The genera *Vitia* (with its synonym *Drymochaera*) and *Psamathia* should be added to the synonymy of *Cettia*. Gladkovaia (Kashin 1977), proposed as a replacement for *Psamathia* which the author believed to be preoccupied by a lepidopteran genus, also becomes a synonym of *Cettia*.

**DERIVATION OF SOUTHWEST PACIFIC CETTIA**

*Cettia parens* and *C. ruficapilla* closely resemble *C. d. seebohmi* of Luzon, while *C. annae* is more similar to *C. d. cantans* of Japan. Palearctic races of *C. diphone*, however, including *cantans*, exhibit strong sexual dimorphism in wing length, a character lacking in tropical Asian *Cettia* including *C. d. seebohmi*. The three Pacific island species exhibit little dimorphism (Table 1; Ali and Ripley 1973, Delacour 1942–43). While sexual size dimorphism may not always increase under island conditions (Selander 1966, Cruz 1977), it is unlikely to decrease. Thus, we believe the island *Cettia* were derived from a tropical, rather than a migratory temperate ancestor. Baker (1951) considered *C. d. seebohmi* a likely ancestor of *C. annae*. We prefer to view *C. d. seebohmi* as bearing a close resemblance to the ancestor of the entire *diphone-annae-parens-ruficapilla* complex. But because *C. d. seebohmi* is a montane endemic confined to Luzon, and thus an unlikely source of a Pacific radiation, we do not share Baker’s (1951) conviction that *C. annae* reached Palau directly from the Philippines. Particularly since *C. parens* and *C. ruficapilla* more closely resemble *C. d.*
seebohmi than does C. annae, we believe the latter more likely colonized Palau from the Papua-Solomons area as did several other species (Mayr 1945, Baker 1951, Ford 1979). Thus, the three Pacific island species can be viewed as relicts of a species of Cettia, allied to C. diphone, once widespread in the Indo-Pacific region.

**EVOLUTION OF CETTIA IN THE SOUTHWEST PACIFIC**

Table 3 presents morphological divergences from Cettia d. seebohmi in males of C. annae, C. parens, and C. ruficapilla. The Pacific species show an 18.3–25.4% increase in relative culmen length and an 8.7–24.4% decrease in relative tail length. No other consistent patterns of change are apparent (contra Baker 1951 in the case of tarsal length), although C. annae shows a 26.6% increase in absolute wing length and a decrease in relative bill width and depth. Even though C. d. seebohmi is not likely the direct ancestor of the Pacific island birds, it probably resembles that ancestor closely enough for differences between it and the insular species to approximate actual evolutionary changes.

Murphy (1938) and Grant (1965) documented increases in bill and tarsus length for insular populations of North American passerines, but noted that these do not always occur together. Grant (1965) postulated that an increase in culmen length was related to the exploitation of a wider range of food items, facilitated by ecological release in a less diverse avifauna. The increased overall size of C. annae may be similarly explained, although it is difficult to see why only this species has so evolved. An explanation for the decrease in tail length is even more obscure. The 24.4% reduction in tail length in C. annae may be related to a retention of juvenal

<table>
<thead>
<tr>
<th>Species</th>
<th>Wing/-wing (%)</th>
<th>Tarsus/ wing</th>
<th>Tail/ wing</th>
<th>Culmen/ wing</th>
<th>Bill width/ wing</th>
<th>Bill depth/ wing</th>
</tr>
</thead>
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<tr>
<td>C. annae</td>
<td>-26.6^a</td>
<td>(-4.5)</td>
<td>-24.4</td>
<td>+20.4</td>
<td>-8.8</td>
<td>-15.8</td>
</tr>
<tr>
<td>C. parens</td>
<td>(+2.5)</td>
<td>(+4.9)</td>
<td>-22.9</td>
<td>+24.6</td>
<td>(+1.8)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>C. r. badiceps</td>
<td>(-2.5)</td>
<td>(+3.9)</td>
<td>-15.0</td>
<td>+19.0</td>
<td>(-3.5)</td>
<td>(-3.5)</td>
</tr>
<tr>
<td>C. r. ruficapilla</td>
<td>(+0.9)</td>
<td>(+0.5)</td>
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<td>+25.4</td>
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<tr>
<td>C. r. funebris</td>
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<td>(+3.9)</td>
<td>-16.1</td>
<td>+18.3</td>
<td>(-3.5)</td>
<td>(+1.8)</td>
</tr>
<tr>
<td>C. r. castaneoptera</td>
<td>(+0.5)</td>
<td>(+1.6)</td>
<td>-8.7</td>
<td>+26.8</td>
<td>(0.0)</td>
<td>(-3.5)</td>
</tr>
</tbody>
</table>

^a Values are the differences between the means for each form and seebohmi, expressed as a percentage of the mean for seebohmi; a positive value indicates a higher figure for the insular forms, a negative value a lower figure; differences of less than ±5% are enclosed in parentheses; presentation modified from Grant (1965).
plumage features suggested by its resemblance to the young of *C. parens*. Wear, complicated by small sample sizes, may have biased some of the results, particularly in *C. parens* ($N = 2$).

We lack the ecological data required to determine whether relationships exist between morphological differences among the three island species and environmental differences among Palau, San Cristobal, and Fiji. The Fiji Warbler, geographically the species most remote from Asia, has diverged least in plumage from the ancestral pattern. A combination of *C. r. badiceps* and *C. r. castaneoptera* might produce a bird differing from *C. d. seebohmi* only in its longer bill, shorter tail, and slightly duller uppersparts. While the larger size of the Palau Bush-Warbler relative to other *Cettia* might be related to the small size of the islands it inhabits, no such island association can be shown among the various subspecies of the Fiji Warbler that occur on islands ranging in size from Viti Levu (10,388 km$^2$) to Kadavu (409 km$^2$).

Unlike *Acrocephalus*, the only other sylviine genus widespread on Pacific islands, *Cettia* appears to have made few adaptive shifts in response to the island environment, probably because no such shifts were necessary. The success of *C. diphones* on Oahu (Berger 1972, Shallenberger 1978) attests to the adaptability of temperate *Cettia* to insular tropical forest communities. In contrast, the reedy and grassy habitats preferred by many continental *Acrocephalus* are scarce on Pacific islands, necessitating a broadening of niche for survival. Noteworthy here is that both the Nightingale Reed Warbler (*Acrocephalus luscinia*) on Saipan (Pratt et al. 1979) and the Carolines Reed Warbler (*A. syrinx*) in the Caroline Islands (Pratt, pers. obs.) occur in forests but are more abundant in thickets and grassy habitats. Holyoak and Thibault (1977) have suggested that *Acrocephalus* has been unable to colonize most of eastern Melanesia because it has been excluded by resident forest-adapted species. *Cettia*, already a forest genus, presumably possessed the necessary preadaptations to establish itself on these islands. Thus, the lack of major habitat shifts in insular *Cettia* should not necessarily be interpreted as indicating a more recent island colonization by that genus than by *Acrocephalus*. In fact, the disjunct distributions of both genera in the Indo-Pacific may indicate a very long period of residence by both.

Gaps in the present distribution of *Cettia* in the southwest Pacific cannot be entirely explained by accidents of dispersal or unsuitability of habitat on the unoccupied islands. In particular, ancestors of *C. ruficapilla* surely reached at least some of the islands between San Cristobal and Fiji, such as the New Hebrides or New Caledonia. Either they failed to establish themselves on these islands, or did so, but subsequently became extinct. The likeliest explanation for their present absence is exclusion by other
species. The Yellow-sided Warbler (Gerygone flavolateralis; Acanthizinae) is common on New Caledonia where it is a bird of forest undergrowth (Delacour 1966; Orenstein, pers. obs.). It is also found in the Loyalty Islands and some of the New Hebrides. Its distribution in the New Hebrides has apparently undergone changes resulting from local extinction and recolonization (e.g., on Santo) in historic times (Diamond and Marshall 1977b). It may therefore have excluded Cettia on islands where it, too, is absent today. On the Santa Cruz Islands, Sanford’s White-eye (Woodfordia lacertosa) may have excluded Cettia. The apparent restriction of C. parens within the Solomons to the highlands of San Cristobal, and, probably, Bougainville, may be the result of diffuse competition (Diamond and Marshall 1977a). Perhaps C. r. funebris is being excluded from the lowlands of Taveuni by the Silktail (Lamprolia victoriae), also an insectivorous understory species. On Viti Levu, where Lamprolia is absent, C. r. badiceps occurs commonly down to sea level (Holyoak 1979; Orenstein, pers. obs.). The present distribution of Cettia in the southwest Pacific resembles that of a population in Stage III of a taxon cycle (Ricklefs and Cox 1972, 1978).

Assigning Vitia and Psamathia to the synonymy of Cettia makes this the only southwest Pacific land bird genus definitely derived from Asia but absent from either New Guinea or Australia. Along with Hirundo, Acrocephalus, Zosterica, and Turdus, it forms one of the few northern elements in an otherwise Australasian avifauna. Whether it is a recent arrival in the area or has been present for a long time, its distribution is of considerable biogeographical, as well as taxonomic, importance.

SUMMARY

The sylviine genera Vitia, with different species on San Cristobal and Fiji, and Psamathia, a monotypic genus endemic to Palau, are here assigned to the subgenus Horeites of the genus Cettia on the basis of similarities in voice, egg color, and morphology. Within Cettia, the species C. annae, C. parens, and C. ruficapilla may share common ancestry with C. diphone. Their continental ancestor probably resembled C. diphone seebohmi of Luzon, but a direct Philippine derivation of these forms is unlikely. A colonization route through Indonesia, with C. annae reaching Palau from the Papuan region, is proposed. The three species may be relics of a single formerly widespread Indo-Pacific species. The insular species have evolved longer bills and shorter tails than C. d. seebohmi. Cettia annae has become significantly larger, and its plumage may represent a retention of juvenile characteristics as shown by the young of C. parens. The Pacific species of Cettia have undergone few shifts in habitat choice. Competitive exclusion may be responsible for the absence of Cettia from suitable islands between San Cristobal and Fiji. The expanded genus Cettia is the only southwest Pacific land bird genus of Asian origin that is absent from New Guinea or Australia.

ACKNOWLEDGMENTS

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SIANA 70893. ACCEPTED 30 NOV. 1982.
DELAYED PLUMAGE MATURATION AND THE PRESUMED PREALTERNATE MOLT IN AMERICAN REDSTARTS

SIEVERT ROHWER, WILLIAM P. KLEIN, JR., AND SCOTT HEARD

The American Redstart (Setophaga ruticilla) is one of about 30 sexually dichromatic North American passerine species in which males exhibit a delayed plumage maturation (Rohwer et al. 1980). Males in their first winter and in their first potential breeding season are largely like females in coloration. These young males have only a few scattered black feathers on their head, back, and breast, areas where adult males are solid black, and they have yellow rather than the orange patches characteristic of adult males in their wings and tail. Two of four hypotheses reviewed by Rohwer et al. (1980) are relevant to the delay in plumage maturation characteristic of these 30 dichromatic passerine species. Both describe hypothesized best-alternative responses by which young males have minimized their disadvantage in one or both forms of sexual competition. The first, which we here rename, is the Cryptic Hypothesis (CH). Selander (1965) developed this hypothesis by arguing that the costs of a conspicuous breeding plumage would not be repaid in yearling males because of their very limited breeding opportunities. This was called the sexual selection hypothesis by Rohwer et al. (1980) and the delayed maturation hypothesis by Procter-Gray and Holmes (1981). The second is the Female Mimicry Hypothesis (FMH). Rohwer and his coworkers (Rohwer et al. 1980, Rohwer 1983) developed this hypothesis by arguing that young males increase their chances of obtaining female-worthy territories and breeding as yearlings by mimicking females and, thus, eliciting less aggression from adult males in the early stages of territory establishment. Both hypotheses assume that breeding opportunities for young males are limited, but the FMH anticipates a substantial effort to breed by first-year males, while the CH anticipates little reproductive effort by yearling males and interprets their developed reproductive tract as a response to occasional opportunistic chances at copulation.

Past hypotheses of delayed plumage maturation have focused exclusively on adaptations relating to the breeding season (Selander 1965, Rohwer et al. 1980, Procter-Gray and Holmes 1981). Here we ask: Is the subadult plumage an adaptation to the first breeding season or is it an adaptation to the first winter season? If subadult plumages are an adaptation to the first winter season, then the major observations past workers have sought to explain are accounted for by the following three-part Winter
Adaptation Hypothesis (WAH): (1) the female-like plumage of young males is of primary (but unknown) functional importance in the first winter; (2) subadult males are simply stuck with their female-like plumage in the first potential breeding season either because they cannot afford a supplementary late winter molt or because such a specialized molt, relevant to only one age and sex class, has been difficult to evolve (see Parkes 1967); and (3) the delayed acquisition of territories by subadults (usually caused by a late spring migration) is an adaptation to reduce aggression from older males, aggression which might be particularly intense because of the inexperience and distinctive appearance of subadult males. This WAH presumes a sexual dichromatism among adults in winter, a point which is true for all of those species listed by Rohwer et al. (1980) (Table 1) as having subadult plumages in their first potential breeding season. Furthermore, the ecology and behavior of adult males and adult females must be different in winter and young males should be more similar ecologically to adult females than to adult males. This WAH would be weakened as an explanation of the breeding season occurrence of subadult plumages if, in late winter, first-year males underwent either a delayed first prebasic molt or a first prealternate molt in which new female-like feathers were grown. On the other hand, the WAH would be supported if a late winter molt produced mostly adult-male-like feathers in species in which first-winter males have a subadult plumage.

In this paper we describe in detail the prealternate molt of male American Redstarts, a species chosen for three reasons. First, redstarts are reported by Dwight (1900) to have a partial prealternate molt, but the molt itself has never been described. Second, because of this presumed molt, data on active molt for redstarts seemed potentially capable of confirming either some breeding season hypothesis (such as the CH or the FMH) or the WAH, depending on the color of actively growing feathers. Finally, relative to adult males, Rohwer et al. (1980) found subadult male redstarts to be more common in western-taken than in eastern-taken samples of museum specimens. This suggested the possibility that some yearling males in eastern populations of redstarts might acquire the definitive breeding plumage for their first (rather than their second) breeding season. Such a bimodal tactic would make good theoretical sense if, for example, early fledged young were competitively more similar to adults than late fledged young (see Rohwer et al. 1980). A bimodal maturation time for young males could be accomplished in either of two ways: first, some young males could molt directly into their definitive basic plumage in the prebasic molt, as is true for the Olive Warbler (Peucedramus taeniatus) (Webster 1958); second, some young males could have a complete prealternate molt, a
### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Subadult males</th>
<th>Adult males</th>
<th>Females</th>
</tr>
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<td>Rictal bristles</td>
<td>Eyes and lores</td>
<td>Other contours</td>
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<td>4</td>
</tr>
<tr>
<td>Feb. 1-13</td>
<td>28.6 b</td>
<td>28.6 b</td>
<td>0</td>
</tr>
<tr>
<td>16-28 20.0 a</td>
<td>20.0 a</td>
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<td>5</td>
</tr>
<tr>
<td>Mar. 1-15</td>
<td>27.3</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>16-31 7.7 a</td>
<td>7.7 a</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>Apr. 1-15</td>
<td>16.6 a</td>
<td>33.3 a</td>
<td>6</td>
</tr>
<tr>
<td>16-30 20.0 a</td>
<td>40.0 a</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>16-31</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>June 1-15</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>131</td>
<td>192</td>
<td>174</td>
</tr>
</tbody>
</table>

* One specimen showing molt in two or three areas.

* Two specimens showing molt in two areas.

Pattern unknown for any parulid (K. C. Parkes, in litt.) but found in two captive, hand-reared redstarts by E. Morton (see Rohwer et al. 1980). We eliminated the first of these possibilities because the prebasic molt occurs on the breeding ground (Petrides 1943) and a direct molt into the definitive plumage by some young males would likely have been discovered either by the collection of molting specimens exhibiting such a transition in appearance or by the discovery of autumn males in full breeding color but without fully ossified skulls. The second possibility, of a complete prealternate molt, could only be evaluated by a study of the reputed prealternate molt.
METHODS

Our results are based exclusively upon the examination of museum specimens. Over 500 specimens from the wintering grounds and over 50 spring and autumn specimens from the eastern United States were examined for molt. The minimum numbers of specimens upon which we have based our conclusions can be deduced from the totals in Tables 1 and 2 and Fig. 1.

All specimens of subadult males that were from the wintering grounds or were presumed to be in migration were checked for evidence of remige or rictrix molt. For all specimens molt on the body was scored in five regions: throat—the anterior undivided portion of the ventral tract; breast—the middle portion of the ventral tract immediately posterior to its bifurcation; sides—the dorsal edges of the posterolateral branches of the ventral tract; head—the capital tract covering the crown of the head; and, back—the anterior portion of the dorsal tract. Using a dissecting microscope, we additionally checked male, but not female, specimens for molt of the rictal bristles and for molt around the eyes and in the lores. Most feathers in all of these body regions were lifted with a dissecting needle to check for small pin feathers or partially ensheathed feathers. To describe body molt quantitatively we used scores of: \(0\) = no molt, \(1\) = one or two growing feathers, \(2\) = three or four growing feathers, and so on to \(5\) = nine or more growing feathers.

For subadult males we quantified the amount of black feathering on the head, throat, back, and breast by measuring the area (mm\(^2\)) covered by black feathers in each of these regions. These measurements were made using a gridded sheet of acetate.

Operational definitions for categorizing specimens into the sex and age classes were: adult males—all birds in the definitive breeding plumage, regardless of the sex indicated on the label; females—only birds sexed as female and completely lacking black feathering; subadult males—all birds showing any black feathering that were not obviously adults and all birds sexed as male but with no black feathering.

Operational definitions for the geographic categorizations of specimens were: breeding grounds—any bird collected from the eastern United States north of the area along the gulf coast in which redstarts do not breed (see Peterson and Peterson 1980); migrants—specimens collected either in Florida or eastern Texas or right along the gulf coast south of the breeding range; wintering grounds—specimens from Mexico, Central and South America, and the West Indies. Obviously some specimens collected on the wintering and breeding grounds were migrating but we made no effort to classify such individuals separately.

To be included in Fig. 1 subadult males from the breeding grounds had to be collected between 1 September and 31 May. These criteria assured that all of the autumn specimens we included were hatched the preceding summer and that all of the spring specimens we included were approximately 1 year old.

RESULTS

If a molt is defined as having either a seasonal or a topographic regularity, then the black feathers that young male redstarts possess on their crown, back, throat, and breast seem not to be acquired in a molt but, rather, to be grown as a consequence of adventitious feather loss. This scattering of black feathers begins to appear in the autumn and slowly increases in number throughout the winter (Fig. 1). The seasonal distribution of specimens showing active molt of body feathers, exclusive of the rictal bristles or the feathers around the eyes or in the lores, suggests the
same conclusion: active feather replacement on specimens from the wintering grounds is rare and occurs from September through April (Table 1). The emergent vane of every partially ensheathed contour feather found on any subadult male examined from the wintering ground was black if it was growing in an area in which adult males are black.

Because of its topographic restriction, the at least partial replacement of the rictal bristles and of feathers around the eyes and in the lores might be considered a limited molt. Replacement of these feathers is somewhat (but not significantly) more intense in subadult than adult males when intensity is measured as proportion of specimens in active molt (19 of 131 vs 15 of 192 wintering specimens; \( \chi^2 = 2.97, \text{df} = 1, P < 0.10 \)). Interestingly, the initiation of this protracted and very limited molt may be delayed in subadult males by about 2 months (Table 1).

The suggestion by Rohwer et al. (1980) that some young male redstarts acquire their definitive plumage in their first winter fails. No specimen
Table 2
Frequencies of Yearling Male American Redstarts That Show Black Feathering Tabulated in Seasonal and Geographic Categories

<table>
<thead>
<tr>
<th>Category</th>
<th>Number with black</th>
<th>Total</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn: breeding grounds</td>
<td>3</td>
<td>26</td>
<td>12</td>
</tr>
<tr>
<td>Autumn: migrants from gulf states</td>
<td>4</td>
<td>12</td>
<td>33</td>
</tr>
<tr>
<td>Wintering grounds: Aug. 1–Dec. 31</td>
<td>27</td>
<td>61</td>
<td>44</td>
</tr>
<tr>
<td>Wintering grounds: Jan. 1–June 1</td>
<td>54</td>
<td>70</td>
<td>77</td>
</tr>
<tr>
<td>Spring: migrants from gulf states</td>
<td>13</td>
<td>13</td>
<td>100</td>
</tr>
<tr>
<td>Spring: breeding grounds</td>
<td>23</td>
<td>24</td>
<td>96</td>
</tr>
<tr>
<td>Total</td>
<td>123</td>
<td>205</td>
<td>—</td>
</tr>
</tbody>
</table>

from the wintering ground was found to be in heavy molt. The highest molt score for all such specimens, including adult males and females, was that of a subadult male taken in December with a score of 12 out of a possible total of 25 (it had feathers growing on the head = 5, chin = 5, and sides = 2). A few subadults had one or more remiges or rectrices with the black and orange coloration characteristic of adults but the distribution of these feathers was always asymmetrical, indicating adventitious feather loss.

On the basis of two subadult males from New York that were growing black feathers in May, Dwight (1900) suggested that the “prenuptial molt” of yearling male American Redstarts took place rather late. Although we have not examined specimens from the breeding grounds for active molt, two points of our data suggest that some additional feather replacement occurs in subadult males as they are moving northward through the continental United States. First, and most importantly, the average amount of black feathering is considerably higher in subadults from the breeding grounds than in subadults taken in late winter or in spring migration (Fig. 1). Second, all but one of the 24 specimens from the breeding grounds that were categorized as a subadult male had scattered black feathering (Table 2). Undoubtedly this frequency change is partly a consequence of more reliable sexing of spring birds but we doubt that more reliable sexing is the entire explanation.

DISCUSSION

This study was undertaken to address two theoretically important questions. First, are young male American Redstarts bimodal in the timing of plumage maturation? Our failure to find evidence of a complete molt in over 130 winter-taken subadult males refutes this possibility. Second, is
the delayed plumage maturation of young male redstarts an adaptation to their first winter season or to their first potential breeding season?

If female-like, rather than adult-male-like, feathers were grown in a late winter prenuptial molt, then the subadult plumage worn by young male redstarts in their first potential breeding season could be inferred to be an adaptation to this first breeding season. Dwight (1900:288) reports that young male redstarts have a limited prenuptial molt and that “new white feathers on the chin are the rule.” Contrary to this statement by Dwight (1900), our examination of specimens for active molt revealed no evidence that male redstarts ever grow female-like feathers after their first autumn. Thus, the molt pattern of American Redstarts fails to confirm either of the summer adaptation hypotheses (the CH or the FMH); although these data cannot reject these hypotheses they do make any explanation of subadult plumages invoking breeding adaptations less credible. Neither a winter nor a summer adaptive explanation of subadult plumages predicted our finding that young male redstarts are physiologically capable of producing black feathers soon after completion of the prebasic molt. Our data do not exclude the possibility that female-like feathers are grown in spring migration after subadults have reached the United States, but this seems most unlikely since some young males have acquired black feathers by August. Such specimens suggest that young males are physiologically “set” to produce black feathers soon after the completion of the prebasic molt.

For three unsatisfyingly weak reasons the subadult plumage of young male American Redstarts can more plausibly be considered an adaptation to their first winter than to their first potential breeding season. First, the absence of an extensive late winter molt in redstarts eliminates a physiological stress that in some species may help force subadults to migrate later in spring than adults. For example, both Purple Martins (Progne subis) and Indigo Buntings (Passerina cyanea) have a partial or extensive late winter molt and in both of these species subadult males return later than adults (Niles 1972, Rohwer and Niles 1979, Carey and Nolan 1979). The absence of an extensive late winter molt in redstarts renders more plausible the argument that the female-like plumage of subadult male redstarts in spring may be a cause, rather than a result, of their late spring arrival (Procter-Gray and Holmes 1981). Second, those feathers around the eyes and in the lores that do seem to be molted in late winter always come in black which is their color in adult males. Third, an explanation of the subadult plumage in redstarts invoking a wintering adaptation is consistent with the fact that winter but not summer subadult plumages occur in the young males of at least some other warblers in which a sexual dichromatism is maintained by adults in winter (e.g., Yellow Warbler [Dendroica petechia], Mourning Warbler [Oporornis philadelphia], and
Canada Warbler [Wilsonia canadensis]). Although this last observation suggests that winter has to be the season to which most immature plumages of male warblers are adapted, it demands an explanation of the absence of a prenuptial molt that would bring young male American Redstarts and Olive Warblers into the definitive plumage for their first breeding season.

We know of only two other studies of the winter molt of species in which males have a subadult plumage in their first potential breeding season, that of Niles (1972) for Purple Martins and Parkes (1967) for eastern Summer Tanagers (Pyranga rubra rubra). Nothing can be concluded from these studies regarding winter vs summer explanations of subadult plumages because the color of incoming feathers on specimens in active molt was not indicated. The mottled appearance of subadult male Summer Tanagers of the eastern race (rubra) and of subadult male Purple Martins proves that they do grow feathers of the definitive plumage in their first winter. While this observation supports the WAH, the evidence is inconclusive for two reasons. First, the possibility that young males also grow female-like feathers in this winter molt has not been excluded for either species; and second, most male Summer Tanagers of the western race (cooperi) are entirely female-like in their first potential breeding season (Rohwer et al. 1980). In summary, no general conclusion concerning the season to which subadult male breeding season plumages are adapted can yet be suggested from interspecific comparisons of molt patterns. Such a comparative study must await quantitative molt studies in those species having both a late winter molt and featuring delayed plumage maturation of males in their first potential breeding season (e.g., various orioles [Icterus spp.], cardinal grosbeaks [Passerina spp., Pheucticus spp.], and tanagers [Piranga spp.]).

Why should the prealternate molt of young male redstarts be limited to the rictal bristles and to the feathers around the eyes and in the lores? A possible explanation is related to foraging needs. The importance of rictal bristles in protecting the eyes of an aerial forager was recently confirmed by Conover and Miller (1980). Many birds have black lores or black feather patches around their eyes. Possibly the function of black color around the eye and, especially of the smooth upper mandible is to reduce glare, thus increasing visual acuity (Burtt 1981). Recently E. H. Burtt (pers. comm.) has confirmed the possible detrimental effect of glare on prey capture in Willow Flycatchers (Empidonax traillii). Individuals with their upper bill painted white foraged more often in the shade than did controls, arguably because their ability to target prey in full sun had been reduced by the experimentally increased glare (Burtt, unpubl.). Given that young male redstarts are physiologically capable of growing black feathers, a limited molt producing black feathers around the eyes may improve the prey cap-
ture rate of young males for their first potential breeding season. Such an explanation presumes that females and first winter males which lack this black feathering forage more in the shade than do adult males; data related to these sex and age differences in foraging ecology do not seem to be available.

SUMMARY

Two seasonal classes of hypotheses may be invoked to explain the delayed plumage maturation of males in sexually dichromatic passerine species. The female-like plumage of first-year males could be an adaptation either to their first potential breeding season or to their first winter. Proof that the female-like feathering is an adaptation to the first potential breeding season would be provided by showing that female-like, rather than adult-male-like, feathers were grown in a late winter molt. This molt could either be a delayed prebasic (i.e., post juvenile) molt as in Purple Martins (Progne subis) or a prealternate molt as occurs in tanagers.

Contra Dwight (1900) no female-like feathers are grown by subadult male American Redstarts (Setophaga ruticilla) in a prealternate molt. Both adult and subadult male redstarts have a very limited prealternate molt involving at least some of the rictal bristles and the feathers around the eyes and in the lores. This molt seems related to increasing foraging efficiency. Contrary to the suggestion by Rohwer et al. (1980), young male redstarts are not polymorphic in the age at which they achieve plumage maturity; young males probably never achieve the definitive plumage in their first prebasic molt and none of over 130 winter-taken first-year males showed evidence of an extensive or a complete prealternate molt. Our data for young male redstarts are more consistent with winter than summer being the season to which their subadult plumage is adapted; however, this conclusion is weak because of the very limited late winter feather replacement in redstarts.

ACKNOWLEDGMENTS

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LITERATURE CITED


FACTORS INFLUENCING THE TIMING, DISTANCE, AND PATH OF MIGRATIONS OF CANADA GEESE

MICHAEL L. WEGE AND DENNIS G. RAVELING

The ability of birds to migrate over long distances has for many years raised intriguing questions concerning the mechanisms of bird navigation. Experiments with caged birds and with artificially displaced wild and domestic species have identified potential orientation cues including landmarks, weather conditions, the sun, stars, geomagnetic fields, inertial forces, polarized light, barometric pressure, and infrasound (see Walcott 1974 and Emlen 1975 for reviews). Field observations have defined times and places of migratory movements and related weather phenomena (Emlen 1975). Few data are available on the exact path flown by individuals for which the origin and destination of migration were known (Griffin 1964, Cochran 1972). Theories concerned with the migration abilities of wild birds ultimately will depend on, and be tested by, such data.

By means of radio-location telemetry, we determined the exact path flown during autumn and spring migration by individual Canada Geese (Branta canadensis) whose destination was known. Knowledge of the destination of a migration flight allowed analysis of the flight path, and nature of the migration (nonstop vs interrupted flight) in relation to weather phenomena and habitat. Autumn and spring migrations were compared with respect to time required for completion, flight corridor, use of orientation cues, and weather patterns.

METHODS

Study areas and population.—Data were collected between 1973–1975 on the population of Canada Geese which nests between lakes Manitoba and Winnipeg in Manitoba, Canada, and migrates to Rochester, Minnesota (Raveling 1976a, b; 1978a). The travels of this population were thoroughly known as a result of color-marking over 1500 birds between 1968–1970 with individually identifiable, plastic neck collars (Raveling 1978a).

Autumn observations in 1973 and 1974 were made at the Marshy Point Goose Sanctuary (50°32'N, 98°7'W) on the southeast shore of Lake Manitoba about 105 km northwest of Winnipeg. This was the main autumn concentration area for the population. The main wintering area for the population was Silver Lake in Rochester (44°N, 92°20'W). Spring observations were made in the Rochester area in 1974 and 1975.

Study animals and transmitters.—Before each migration season, previously neck-banded geese with a history of migrating between Marshy Point and Rochester were captured in a drop-gate, walk-in trap or with a cannon net. These geese were outfitted with transmitters contained in a harness design that was modified from Cochran et al. (1963) and Raveling (1969) to accommodate a rigid, 30.5-cm whip antenna to increase signal strength. Total weight of transmitters (including harness) varied from 50–75 g (which was 1–3% of adult body weight) depending on the size and number of batteries used.
Social status and migration categories.—Daily observations with a spotting scope allowed the determination of the social status of most of the neck-banded geese on the study areas. Individuals were classified into three social categories (single, pair, or family; see Fischer 1965; Raveling 1969, 1970) and five migration departure and arrival categories based upon the migratory pattern of the total population (before first wave, first wave, between first and second wave, second wave, and after second wave).

Migration monitoring.—Migrations of transmitter-tagged geese were monitored with the use of a ground vehicle, an airplane, ground observers, and a base station (see Cochran et al. 1967). All times are Central Standard Time (CST).

Weather.—Weather conditions were recorded during migration flights and additional data were obtained from weather stations located along the migration route (Winnipeg, Manitoba; Grand Forks and Fargo, North Dakota; Thief River Falls, Detroit Lakes, Alexandria, St. Cloud, Minneapolis, Redwood Falls, and Rochester, Minnesota). Wind directions, unless otherwise indicated, were the directions from which the wind was blowing.

RESULTS

Autumn Migration

Timing.—Although some migration occurred almost continuously between 20 September and late November, the bulk of the population migrated in two brief periods (2–6 days each). These wave-like departures from Marshy Point were reflected in censuses taken in Rochester (Table 1). Departure waves occurred 14–15 October and 2–4 November 1973 and between 28 October–2 November and between 8–13 November 1974. Arrival waves at Rochester occurred during 14–20 October and 2–6 November 1973 and during 1–6 and 11–18 November 1974.

Nonstop vs interrupted migrations.—Data on the nature of the complete migration were obtained for seven transmitter-tagged geese in 1973 and for eight in 1974. In 1973, four of seven birds completed the 855-km trip in a nonstop flight. In 1974, however, only one of eight birds migrated nonstop. The range in flight time for these nonstop migrations was 7 h 52 min–11 h 38 min.

The 10 birds making an interrupted migration took 1–12 days to complete the migration. The magnitude of this range is misleading as, except for two birds which left during the final departure from Marshy Point (18 November 1973 and 13 November 1974), the migration was completed by the others in 1–2 days. The two birds departing at the end of the migration season took 8 and 12 days, respectively.

Nonstop or interrupted migrations did not appear to be related in any obvious manner to social status or departure date (i.e., migration category). The social status of five nonstop migrants included: family (3), pair (1), and unknown (1). Status of the 10 geese which did not migrate nonstop were: family (4), single (2), pair (1), and unknown (3). The migration category for nonstop migrants included three departures during the first wave and two during the second wave of migration. Four interrupted migrants
Table 1

ARRIVAL OF CANADA GEESE AT ROCHESTER, MINNESOTA

<table>
<thead>
<tr>
<th></th>
<th></th>
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<tbody>
<tr>
<td>20–30 Sept.</td>
<td>19,440</td>
<td>20,670</td>
<td>23,640</td>
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</tr>
<tr>
<td>1–10 Oct.</td>
<td>9b</td>
<td>4</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>11–20 Oct.</td>
<td>12</td>
<td>6</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>21–31 Oct.</td>
<td>22</td>
<td>48</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>1–10 Nov.</td>
<td>9</td>
<td>10</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>11–20 Nov.</td>
<td>22</td>
<td>32</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>21–30 Nov.</td>
<td>4</td>
<td>—</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

a 1968–1972 data from Minnesota Department of Natural Resources and Raveling (unpubl.); 1973 and 1974 data from present study.

^ Figures represent the percent of the peak population censused at Rochester in late November that arrived during that time period.

departed during the first wave, five during the second wave, and one after the second wave of migration. Nonstop flight departures occurred after sunset (20:15–22:22) and during mid-morning (08:00–10:03). While 2 of the 10 geese which interrupted their flight departed during mid-morning (08:00–09:30), six departed during mid-afternoon (13:05–14:58) and two after sunset (19:30–19:55). In addition, 8 of the 10 interrupted migrations were completed during daylight hours in contrast to the nocturnal flights of three of the nonstop migrants.

Migration onset time.—The time of departure for transmitter-tagged birds showed a similar pattern in both years. Departures in October occurred after sunset (19:30–22:22, N = 5), while all recorded departures in November occurred during the day (08:00–14:58, N = 8).

Migration path.—We characterized the autumn flight corridor as containing two sections: (1) from Marshy Point to the northwest corner of Minnesota; (2) from northwest Minnesota to Rochester (Fig. 1). The first migration section was similar for all flights as all geese that were tracked in this area (N = 7) flew 10–35 km west of Winnipeg. The points (N = 4) where transmitter-tagged geese crossed the Manitoba-Minnesota border were within 25 km of one another. The second section of the migration corridor steadily increased in width until it reached a maximum of 210 km between Minneapolis and Redwood Falls. The autumn migration corridor was generally located along the forest-prairie ecotone in Minnesota (see Taylor and Ludwig 1966, Wilson and Loomis 1967 for descriptions). The eastern and western boundaries of the corridor were the paths of diurnal flights of individuals that stopped before reaching Rochester.
Fig. 1. Autumn migration flight corridor encompassing the 10 paths flown by transmitter-tagged Canada Geese.
Weather.—All 13 transmitter-tagged geese departed with a following surface wind, decreasing daily mean temperature, and increasing barometric pressure. Increasing relative humidity and no precipitation occurred during nine departures and eight occurred with a clear to partly cloudy sky.

The sun, moon or stars were visible for at least part of the time for 11 of the 13 tracked migration flights. Interrupted flights occurred with more and lower clouds than did nonstop flights (with one exception when a nonstop flight occurred during rain and low clouds; see Wege 1979 for more details on weather). After-sunset departures (N = 5) were within 4 days after a full moon and within 5 h after moonrise.

The enroute weather conditions encountered by transmitter-tagged birds differed for nonstop and interrupted flights. Three of the four nonstop migrations in 1973 were overnight flights made under favorable conditions of a following surface wind (270°–360°, 11–37 km/h), increasing barometric pressure, no precipitation, and a clear to partly cloudy sky. Two nonstop flights occurred during daylight under poorer conditions with the presence of rain, snow, and an overcast sky. Interrupted flights occurred when birds encountered snow (N = 3) or the onset of darkness (N = 5). Weather data at the time of interruption were available only for eight geese. Three of the 10 birds completed the migration on the following day while five birds took from 2–12 days. The time of completion of migration was not determined for two birds. Two of the three birds that completed the migration within 24 h had landed in northwestern Minnesota at sunset and departed on the following day with weather conditions that were favorable and similar to those at departure (decreasing temperature, increasing barometric pressure, following surface wind at 13–20 km/h, no precipitation, and a partly cloudy to overcast sky). The remaining bird landed after encountering snow along the Manitoba-Minnesota border, but resumed its migration on the following day when conditions improved (i.e., no precipitation, clear sky, following surface wind at 7–18 km/h). Of the five birds that took more than one day (i.e., >24 h, but 2 or more calendar days) to complete their migration, two stopped at sunset, one stopped 3 h after sunset, and two stopped after encountering snow around 22:00. The latter birds resumed their flight after the snow ended.

The last departing geese in both 1973 and 1974 took the longest to complete their migrations (12 and 8 days, respectively). In 1973, variable weather conditions including snow, head winds, and decreasing barometric pressure occurred at the stopover site between the 18 November departure date and 28 November. On 29 November a high pressure system with accompanying stable air including a wind shift from south to north,
an end to the precipitation, a clear sky, and increasing barometric pressure moved into the area. Favorable conditions continued on 30 November when the migration was completed. A similar pattern occurred in 1974 when a bird remained at its stopover area from 13 November until a stable high pressure system moved in on 19 November when it then continued its migration. However, the migration was not completed until 21 November, even though conditions had remained favorable.

Spring Migration

Timing.—At the onset of thawing in late February or early March, geese dispersed from Silver Lake. Because geese no longer concentrated daily at Silver Lake, it was difficult to accurately census the population and to detect minor migration departures. Major departures of geese (i.e., >5000) were observed on 2 and 6 April 1974, and between 12 and 14 April 1975. The major departures of geese included 14 of 23 and 11 of 17 transmitter-tagged geese in 1974 and 1975, respectively. Major arrivals on the nesting grounds occurred from 8–12 April 1974 and 13–15 April 1975.

All spring migrations of radio-tagged geese were interrupted. The mean duration from departure from Rochester to arrival at Marshy Point, Manitoba was 10 days in 1973 (range = 6–14 days, N = 3) and 7 days in 1974 (range = 6–9 days, N = 4).

Migration onset time.—As observed in autumn, departure times occurred earlier in the day as the season progressed for the 1974 spring migration. The second major departure (6 April) occurred between 06:00–12:00, whereas previous departures were 17:50 on 13 March and 15:30, 16:00, and 17:00 on 2 April. This trend was not evident in 1975 as departures occurred at 04:55 on 8 April, 18:15 on 12 April, 04:00, 06:30, 16:30 on 13 April, and 06:40 on 16 April.

Migration path.—The spring migration path followed an arc from Rochester west-northwest through western Minnesota and eastern North Dakota, and then north into central Manitoba (Fig. 2). Stopover areas were pastures and grain fields containing water from snow melt.

Weather.—Major departure from Rochester in 1974 occurred when major rivers were free of ice in southern and southwestern Minnesota and melt water was abundant in western Minnesota and eastern North Dakota. Because the ground was still frozen, the water from melting snow gathered in low lying areas among the rolling hills of this area. Lakes and marshes located in the more vegetationally closed forest-prairie ecotone area in Minnesota (see Fig. 2) were still frozen. The departures of 11 transmitter-tagged geese that were tracked occurred under generally similar weather conditions, although there was greater variation in these conditions than was found for autumn departures. No precipitation and a following surface
Fig. 2. Spring migration flight corridor encompassing the 16 paths flown by transmitter-tagged Canada Geese.
wind (60°–190°) occurred during 10 departures; nine migrations were initiated when the daily mean temperature was increasing; seven departures occurred with a completely overcast sky, and increasing relative humidity; and six occurred with decreasing barometric pressure.

On eight occasions, weather conditions encountered enroute by transmitter-tagged geese were recorded. They were similar to conditions at departure and included: seven occasions with no precipitation and decreasing barometric pressure, five with an increasing daily mean temperature and a following surface wind, four with increasing relative humidity and an overcast sky.

The weather conditions existing when spring migration flights were interrupted were recorded for five transmitter-tagged geese on six different occasions. Birds landed with continuing favorable conditions at 12:00, 13:00, 14:00, 18:30 (sunset), and 22:30; and with deteriorating weather (wind shifted to northeast and rain began) at 15:30.

The visibility of the sun, moon or stars was similar for spring migration flights in both 1974 (N = 11) and 1975 (N = 7). The total sample size (18) is greater than the number of birds tracked (N = 11) because some geese were tracked more than once before reaching their breeding grounds (i.e., they had interrupted their migration). The only after-sunset departure (in 1974) occurred after the setting of a half-moon under partly cloudy skies so that some stars were visible. Three 1974 daylight departures occurred under complete overcast, however, the sunrise had been visible, as had been the moon during the previous night. The other seven departures in 1974 occurred when the sun was visible. Similarly, 1975 departures under overcast conditions occurred after: (1) the sun and moonrise were visible during the previous day (N = 2); (2) the sunrise was visible on the day of departure (N = 1); and (3) complete overcast had obscured the sun and moon during the previous 2 days, except for the sun being visible for 3 h under 3/10 cloud cover on the day before departure (N = 1). In general, the sun or moon and stars were visible during more than one-half (N = 10) of the flights and there was no precipitation during 17 of the 18 migration flights but many clouds were present during 14 of the flights.

DISCUSSION

Autumn vs spring migrations.—In autumn, this population tends to migrate between wildlife refuges which provide protection from hunters and to minimize the number of migration stopover locations (Raveling 1978a). Autumn migrations during this study tended to be characterized by direct flight paths, nonstop flights when departure time and weather conditions permitted, and the resumption of interrupted migrations as soon as weath-
er conditions permitted. The last major departure of geese from Marshy Point occurred 2–3 days before final freeze-up of the marsh. Therefore, autumn migrations preceded the time at which water roosting areas became totally unavailable.

Successful reproduction in northern geese requires that nesting begin almost as soon as nest-sites become available in spring (Cooch 1961, Barry 1962, MacInnes 1962, Raveling 1978b). A delay in egg-laying due to a late spring thaw or to a goose not being in the proper physiological condition increases the probability of nesting failure (Cooch 1961, Barry 1962). Despite the relatively short distance between wintering and breeding areas (855 km) for this segment of the Giant Canada Goose population, spring phenology, and weather conditions experienced upon arrival on the breeding grounds are comparable to arctic nesting geese (see Cooper 1978:20). Although renesting may occur in this population, initial nesting attempts coincide with newly available nest-sites and open water (Cooper 1978) as reported for more northern geese (see above references).

Arrival on nesting grounds in close synchrony with soon to be available nest-sites involved undertaking short flights with favorable weather conditions to prairie locations offering open water. Initial migration flights were shorter and more days were required to complete spring migrations ($\bar{t} = 8.3$ days, range 6–14 days) than were recorded for autumn migrations ($\bar{t} = 2.3$ days, range 0.33–12 days) ($t = 3.65, P < 0.01$). Reverse migrations in spring occurred when geese were confronted with the lack of open water and food. Reverse migrations also occurred in autumn (Raveling 1976b).

**Flight corridor.—** The autumn migration corridor along the forest-prairie ecotone (Fig. 1) provided numerous suitable wetland stopover areas for migrating geese and a minimal energy expenditure as a result of a nearly direct flight path to their destination. The prairie to the west contained many fewer water areas in autumn. The spring migration corridor was 20–55 km west of the autumn corridor (Fig. 2). Two factors combined to cause suitable stopover areas to be first located in southwestern and extreme western Minnesota and eastern North Dakota. Firstly, spring storms passed through the Midwest on a generally southwest to northeast line (Barry and Chorley 1971:227). Secondly, the habitat in these areas was tall grass prairie (presently, cultivated grains and pasture). The rain and warm temperatures of spring storms, along with the open habitat, caused the early formation of melt water in pastures and grain fields. Snow melt and ice thaw on marshes and lakes occurred in the more closed conditions and permanent water bodies of the forest-prairie ecotone after spring migration had been completed. Therefore, open water and food were unavailable
and this area was little used during spring. However, similar to autumn, the spring migration corridor was the most direct suitable path to the breeding grounds, resulting again in a minimum of expended energy.

Orientation cues.—The use of landscape features is variable among species and may be most important during migration in locating a specific wintering or breeding site (Bellrose 1972, Keeton 1974, Emlen 1975, Wiltschko and Wiltschko 1978). For nocturnal-diurnal migrants (e.g., Canada Geese), Bellrose (1967, 1972) concluded that landscape features were most important in maintaining the flight direction during diurnal flights. Visual cues provided by open water and cities could have been used to maintain the migratory direction by the geese in this study. In autumn, permanent lakes along the forest-prairie ecotone and the Red, Mississippi, and Minnesota rivers (Fig. 1) and, in spring, patterns of ice-free rivers and melt water in fields could have provided critical landscape cues. The paths of two birds which approached Rochester from the southwest, and one bird which followed the Mississippi River suggest that local landmarks influenced their final approach. One of these geese approached Austin (Fig. 1) from the north-northwest and when it was about 13 km north of the city, changed course abruptly and flew northeast for 28 km until encountering Rochester where it then landed at a small lake located in the southwest part of the city. The sky was completely overcast at the time but the cloud ceiling was 24,000–32,000 m with 25–30 km surface visibility. The second bird approached Austin from the west-northwest and, when it was about 6 km south of the city, turned and flew northeast. After flying 44 km it landed at Rochester. The sky was again completely overcast, and the ceiling (2200–3200 m) and visibility (15–20 km) were reduced. Austin may have been confused with Rochester by these birds. These two towns are similar in size and larger than any other town in this area of southeastern Minnesota.

Research has tested the effect of the earth’s magnetic field on a bird’s orientation ability, but little discussion has addressed the possible importance of the magnitude of magnetic activity in determining the time of migration departures (Richardson 1974, 1976). Multivariate analyses of 33 weather variables revealed that magnetic disturbance was correlated with migration departure (Wege 1979).

Variation within migrations.—While autumn and spring migrations were related to favorable weather periods, there was variation in departure and arrival dates of migration waves and in flights of transmitter-tagged birds. Band recoveries and previous field observations indicated that the autumn migration occurred between 20 September and 20 November and tended to be nonstop. About one-half of the population migrated by 1 November and about 66% of the population arrived at Rochester during two periods (10–20 October and 1–20 November) (Table 1). Major arrival in 1973 was
the earliest and largest recorded between 1968–1974, while that in 1974 was the second latest.

The sequence of events during the 1975 spring migration demonstrated that the time required to complete the migration may be shorter in a late spring. The major departures from Rochester averaged 9 days later in 1975 than in 1974, but the major arrival at Marshy Point was only 4 days later. The apparent reduction in migration time is further indicated by the fact that transmitter-tagged geese took an average of 10 days to complete the migration in 1974 ($N = 3$) and 7 days in 1975 ($N = 4$). There was little delay in reproduction as the first egg was laid at Marshy Point just 1 day later in 1975 than in 1974.

Transmitter-tagged geese.—For the 1973 and 1974 autumn and the 1974 spring migrations, departures of transmitter-tagged geese were nocturnal early in the migration season and then diurnal later in the season. This change cannot be explained by any readily apparent difference in nocturnal vs diurnal weather conditions. Perhaps there are both nocturnal and diurnal migratory individuals or segments of the population, with the nocturnal geese tending to be early season migrants. Support for such an hypothesis comes from the fact that individuals (neck-banded) began migration in the same relative order each year (Wege 1979), and the interruption of migration around sunset by diurnal, transmitter-tagged migrants occurred on five of eight occasions (the other three interruptions occurred when geese encountered a snow storm). All eight of these geese completed their migrations with only diurnal flights.

No transmitter-tagged geese interrupted their migration at sunrise. Since all recorded nocturnal departures occurred before midnight, geese that flew all night were at least 75% of the way to Rochester by sunrise and would be able to complete their migration within a few hours. Bellrose (1964) observed that before nocturnal migrating waterfowl made a major change in direction, it appeared they needed to obtain landscape cues during the day. Similar behavior by geese in this study was not observed either because no major changes in direction were required and the recognition of local landmarks was sufficient to make minor changes in direction and to guide them to Rochester, or because migrating geese were readily able to change from using astral cues to celestial or landscape cues. The flight paths of three nocturnal, nonstop migrants indicated that an almost direct flight line was maintained between Marshy Point and Rochester.

SUMMARY

Canada Geese (*Branta canadensis*) with a known history of migrating between Marshy Point Goose Sanctuary, Manitoba, and Rochester, Minnesota, were fitted with 50–75 g radio transmitters between August 1973 and April 1975. Part or all of the migrations of 25 indi-
individuals were tracked with a ground vehicle and an aircraft. Autumn migrations were characterized by a relatively direct flight path, nonstop flights when departure time and weather conditions permitted, and the resumption of interrupted migrations as soon as weather conditions permitted. Spring migrations involved shorter flights along the edge of the snow melt which facilitated arrival on the nesting grounds in close synchrony with soon to be available nest-sites. There may be nocturnal and diurnal migratory individuals or segments of the population, with the nocturnal geese tending to be early season migrants.

The autumn migration corridor was on a direct path between Marshy Point and Rochester and was generally located along the forest-prairie ecotone in Minnesota where water was available in permanent potholes. Due to the path of spring storms in the Midwest and because snow on the prairie melted earlier than ice on the potholes, the formation of melt water occurred first on the prairie. The spring migration corridor was associated with this open water and was 20–55 km west of the autumn corridor. Thus, patches of open water served as major visual cues influencing the migration path. The paths of three birds indicated that the recognition of local landmarks probably determined their final approach to their destination. During nocturnal flights, when these landscape features may be unavailable, astral cues were available.

ACKNOWLEDGMENTS

We gratefully thank the P. D. Curry and A. J. Vincent families on whose property geese were trapped in the autumn. Several agencies and individuals provided generous help and included: R. Johns of the Canadian Wildlife Service; Manitoba Department of Mines and Natural Resources; R. Vose and R. Bilder of St. Mary’s College, Winona, Minnesota; R. J. Christman of Macalester College, St. Paul, Minnesota; S. Fritts of the U.S. Fish and Wildlife Service; W. W. Cochran of the Illinois Natural History Survey, Urbana, Illinois; P. McFall and A. Stegen of the Minnesota Department of Natural Resources; M. R. and I. McLandress, L. Salata, S. Paulus, and T. R. Akesson of the University of California, Davis, California. R. G. Schwab and W. J. Hamilton, III, reviewed earlier drafts of the manuscript. K. F. Abraham and C. D. MacInnes also provided helpful review of the paper. This study was funded by a grant from the National Science Foundation (GB-38788).

LITERATURE CITED


WINTER BEHAVIOR OF TUFTED TITMICE

JEFFREY D. BRAWN AND FRED B. SAMSON

Tufted Titmice (Parus bicolor) are non-migratory woodland birds widely distributed in the midwestern and eastern United States and are at present expanding their range northward (Gosselin and David 1980). Despite extensive studies of North American (Dixon 1956, Glase 1973) and Eurasian congeners (Perrins 1979), little intensive research has been done on this common species and information concerning behavior outside the breeding season is often contradictory and incomplete. For example, Wilford (1977) reported that, in winter, Tufted Titmice do not form cohesive groups and individual titmice are either transient or local permanent birds; whereas Gillespie (1930) and Condee (1970) found titmice in winter flocks with stable territory boundaries. Furthermore, little work has been done on the nature of social interactions among wintering titmice.

The primary purpose of this study was to investigate winter behavior of Tufted Titmice. The objectives of this study were to determine (1) whether birds formed social groups during the non-breeding season; if so, (2) the sex and age of group members; (3) patterns of social dominance within groups; and (4) fate of group members during the ensuing breeding period.

STUDY AREAS AND METHODS

The study was conducted in central Missouri from October–June 1977–78 and September–May 1978–79 in a 16.5-ha area of mature, undisturbed oak-hickory forest within the Rock Bridge State Park (RB), Boone Co., and in an area similar in size and species composition but intensively managed in the U.S. Forest Service Cedar Creek Management Area (CC), in Callaway County (Fig. 1). White oak (Quercus alba), black oak (Q. velutina) and hickory (Carya spp.) were dominant on upland ridges and American sycamore (Platanus occidentalis) and green ash (Fraxinus pennsylvanica) on bottomland areas. Scattered honey locust (Gleditsia triacanthos) and eastern redcedar (Juniperus virginiana) were present in old-field habitat. Both study areas were surrounded by similar habitat, cultivated farmland, pasture, and urban development.

Mark and capture of birds.—Titmice were banded with USFWS numbered bands from late September–January (1978) or February (1979) and all trapped individuals received unique combinations of colored plastic leg bands. In addition we marked the titmice during 1978–79 by painting with model airplane paint the ventral side of retrices with individualized patterns to facilitate identification of birds at a distance (Dixon 1956). Titmice were captured in eight Potter traps baited with sunflower seeds. Traps were moved frequently to avoid influencing movement or behavior of the titmice. The total trapping effort consisted of 270 trap-h on RB and 230 h on CC in 1977–78 and 175 h (RB) and 125 h (CC) in 1978–79. Birds were sexed by length of wing chord (N = 26) or observation of breeding activity (N = 5) and aged by examination of skull ossification and bill color (Condee 1970). Titmice sexed in fall and winter and found in spring proved by wing measurement to have been correctly determined.
Distribution of birds in winter and fall.—The study areas were marked with colored marker flags at 40-m intervals; thus, we could map locations of individual titmice. In winter, each study area was surveyed 2–3 times/week during which we recorded the locations and movements of titmice. We devoted particular effort to mapping the locations of aggressive encounters between birds and recording the identity of birds in association with other titmice. Observations were transferred to composite maps for each individual and/or group of birds. Distances travelled and areas occupied during winter were calculated with a planimeter.

We determined the fate of titmice marked in winter by searching the study areas and surrounding areas at least twice weekly from March–June (1978) and May (1979). The location and identity (when possible) of singing males, pairs observed in courtship feeding, and birds involved in inter-male aggression were mapped. The area of an individual breeding territory was delineated by the polygon of outermost points, all of which had been recorded before the end of April.

Determination of dominance hierarchies.—In this study we follow Morse (1970:120) in defining a flock as “Any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species.”

Dominance hierarchies within the flocks that we detected were determined by observation of behavioral interaction between titmice on and off bait-sites. Bait-sites consisted of suspended 1-m² platforms covered with sunflower seeds. A minimum of 10 observation periods (15 min each) were held at bait-sites within the territory of each flock during which we recorded the number of times each titmouse successfully acquired a seed. Bait-sites were moved frequently and observation periods were held only when all flock members were present. Data from observation periods were analyzed by averaging the number of seeds acquired/bird/period and testing for differences between birds with Kruskal-Wallis and multiple comparisons tests (Conover 1971).

Behavior away from bait-sites was recorded by documenting cues to dominance such as supplanting, chasing, “facing off,” and “appeasement” (Dixon 1956, Glase 1973). During
such bouts the birds involved were scored as either winners or losers. Encounters resulting in no apparent winner were scored as a tie (Ketterson 1979). Data obtained on and off bait-sites were then used to rank each titmouse within a flock.

RESULTS

Thirty-five titmice were trapped and marked on the study areas. Nine juveniles either settled on areas off the plots or were not observed subsequent to being marked. Disappearances occurred early in the field seasons (September–October) during periods when there was considerable movement of titmice.

Flock structure.—Titmice which remained on the plots formed 14 flocks. We found, during both winters, four flocks on the RB plot and three on the CC plot. The flocks began to form in September and membership was stable by late October in both years. We were unable to identify the age and/or sex of one or more individuals in six of the flocks. One bird remained unbanded on CC during the 1977–78 winter. Fifteen titmice trapped and marked during the first field season were still present on the study areas during the 1978–79 winter.

The number of birds per flock ranged from 2–5 with two being the modal flock size (Table 1). All flocks consisting of two birds, in which we were able to identify the sex of both individuals, were comprised of one male and one female. Overall, males outnumbered females in the flocks for both the adult and juvenile age classes. In the flocks where all individuals were aged the adult : juvenile ratio was 1.42:1. Only one flock contained more than one adult male and no flocks contained more than one female of either age class.

The composition of the flocks was stable throughout the flocking period. We did not observe any additions to any flock after mid-October, although there may have been movement of unbanded birds. Seven marked birds did disappear from the flocks. We found the remains of three titmice (feathers, but no bands) and it is likely that these birds were preyed upon by Sharp-shinned Hawks (Accipiter striatus) that were observed on the

<table>
<thead>
<tr>
<th>No. of ind./flock (N = 14)</th>
<th>Adults (N = 8)*</th>
<th></th>
<th>Juveniles (N = 8)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males/flock</td>
<td>Females/flock</td>
<td>Males/flock</td>
<td>Females/flock</td>
</tr>
<tr>
<td>∧</td>
<td>2.9</td>
<td>1.13</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Range</td>
<td>(2–5)</td>
<td>(1–2)</td>
<td>(0–2)</td>
<td>(0–1)</td>
</tr>
</tbody>
</table>

*Sample size indicates number of flocks in which all members were aged and sexed.
plots during both winters. None of the birds that disappeared were found on nearby areas or elsewhere.

*Flock territories and movements.*—The average size of the flock territories was 5.4 ha (Fig. 2). The territory boundaries were stable and defined early in the flocking period. The size and configuration of the territories were similar between the two field seasons on both plots (1977–78: $\bar{x} = 5.33$ ha, $N = 7$; 1978–79: $\bar{x} = 5.47$ ha, $N = 7$, NS, Wilcoxon Signed Rank Test). The size of the flocks and of their territories were not significantly correlated ($P = 0.29$, $N = 14$, NS, Spearman’s Rho).

Inter-flock aggressive behavior, which was observed 41 times, occurred on or near territory boundaries (Fig. 2). These disputes occurred between males in 38 (93%) of the cases observed and were characterized by loud vocalizations and relatively “excited” behavior. We occasionally saw single birds within a neighboring territory. The intruders, always males, either quietly returned to their own territory or were driven off by residents.

Within their flock territories the titmice travelled singly (20% of all observations), in pairs (65%), or in groups of three or more (15%). The flocks which contained four or five individuals were cohesive early in the day (06:00–09:00) and later fragmented into pairs or single birds. Similar patterns of flock cohesion have been reported by Austin and Smith (1972). All birds were observed throughout their flock’s territory. However, it appeared that within the larger flocks ($\geq$3 individuals, $N = 8$) pairs, com-
prised of one female and male, preferred certain portions of their flock’s territory for winter activity.

The titmouse flocks preferred forested areas to the more open old-field habitat. Mature bottomland habitat appeared to be favored when the titmice were foraging. In addition, during especially windy, cold weather the titmice would habitually seek the riparian areas where vegetation (canopy trees, shrub layers) was particularly thick.

Social dominance within flocks.—The intra-flock dominance hierarchy was linearly peck-right (Table 2); that is, each member of a flock was consistently either dominant or subordinate to its fellow flock members once the hierarchies became established. Dominance patterns were not site specific. Males were generally dominant over females and, within a sex, adults over juveniles. An exception to this was in the CC3:77-78 flock, in which an adult female was dominant over a juvenile male.

Flock members could be consistently ranked according to the results of the 15-min observation periods. The ranks assigned to a bird based on behavior observed away from bait-sites were consistent with the data from the observation periods. Kruskal-Wallis and multiple comparisons tests indicated that the mean number of seeds acquired/bird/observation period was not significantly different between birds in flocks of three members or less. In the larger flocks (N = 4) the alpha (i.e., most dominant) males acquired a significantly greater number of seeds/observation period ($P < 0.05$) than the birds with the lowest social status.

Social dominance, within a sex, appeared to be a function of seniority on the flock territory. During the 1978–79 winter all of the alpha males and females were birds that had bred (as pairs) during the previous spring on areas within their flock’s territory. The determination of dominance among
juveniles of the same sex was also governed by seniority on a flock territory. Three juvenile males that gained membership to flocks early in the fall were dominant over other juvenile males that joined the same flock later.

**Fate of flock members during the breeding period.**—In late February and March, male titmice began to give the characteristic *peto-peto* breeding vocalization and courtship feeding was observed. Courtship feeding was useful in determining the sex of individuals whose sex was previously unknown.

Alpha males and females became or proved to be paired together in 12 of the 14 flocks. These pairs were the first (N = 5) or only (N = 7) to breed within their respective flock territories. Two exceptions to this pattern were found: (1) the RB3:77–78 flock in which the alpha female disappeared and the alpha male paired with a subordinate female; and (2) the CC3:78–79 flock in which the alpha male disappeared and the beta male paired with the alpha female. These two pairs were also the first titmice to initiate breeding within their flock territories.

The fate of subordinate individuals during the breeding period (N = 9, both years pooled) was more variable. Three females and two males remained on their flock territories and were observed with mates. Two females, one juvenile and one of unknown age, emigrated off their flock territories and found mates. Two males were not seen with mates and were seen on and off their flocks’ territories.

The titmice preferred fellow flock members as mates. All of the alpha males and females and four of the seven subordinate birds that became paired did so with members of their flocks of the previous winter.

During the spring the flock territories supported one or two breeding pairs (Fig. 3). The number of breeding pairs supported in each flock territory was the same during the two breeding seasons.

The alpha pairs established territories from 3–4 weeks earlier than the second breeding pairs on a flock territory (Table 3). Titmice that emigrated off their flock territories, and found mates, established territories 4–5 weeks after their flock’s alpha pair.

**Feeding associates.**—The titmouse flocks in this study were essentially single-species flocks. We did not observe the titmice actively participating in the mixed-species flocks that were present on both study plots. The mixed-species flocks varied in composition but typically included the Black-capped Chickadee (*P. atricapillus*), Yellow-rumped Warbler (*Dendroica coronata*), Downy Woodpecker (*Picoides pubescens*), and Brown Creeper (*Certhia familiaris*). Titmice occasionally travelled with the mixed-species flocks when such flocks were present within their territories. Titmice did not leave their flock territories in association with the mixed flocks.
DISCUSSION

The participation of Tufted Titmice in winter flocks was clearly evident in our study. The aforementioned confusion concerning titmouse social behavior in winter likely arose from the following: (1) winter flock size is variable and may be as small as two birds, (2) the cohesiveness of flocks varies throughout the day, and (3) pairs of titmice within flocks comprised of three or more birds favor certain areas within their flock territories. Samson and Lewis (1979) found that titmouse flocks in Pennsylvania were comprised of up to eight birds but noted that no pairs traversed the entire flock range. Our study and that of Samson and Lewis (1979) suggest that, regardless of size, the pair is the basic social unit in Tufted Titmouse flocks (sensu Saitou 1978). Certain pairs accept other titmice on their winter range and other pairs remain alone throughout the winter.

Winter flocks of Tufted Titmice and those of other congenic species appear to have several characteristics in common. A linearly peck-right social hierarchy with dominance governed by sex and seniority within the flock territory is typical of species in Paridae (Odum 1941, Hinde 1952, Dixon 1956). Virtually all studies of parid flocks in which social dominance patterns were delineated indicate that alpha males and females remain within a winter flock territory to breed. If present, subordinate birds usually disperse, but may remain within their flock territories if they become paired with a fellow flock member (Hartzler 1970, Glase 1973, Smith 1976).
Table 3
Characteristics of Breeding Territories of Dominant and Subordinate Tufted Titmice

<table>
<thead>
<tr>
<th>Study plot and year</th>
<th>Position in social hierarchy</th>
<th>Mean date of establishment</th>
<th>Mean size (ha)</th>
<th>Mean linear distance from center of flock territory to center of breeding territory (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC:78-79 Dominant pair</td>
<td>13 April</td>
<td>3.6</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>CC:78-79 Subordinates</td>
<td>29 April</td>
<td>3.8</td>
<td>675</td>
<td></td>
</tr>
<tr>
<td>CC:78-79 Dominant pair</td>
<td>4 April</td>
<td>3.4</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>CC:78-79 Subordinates</td>
<td>8 May</td>
<td>3.4</td>
<td>598</td>
<td></td>
</tr>
<tr>
<td>RB:77-78 Dominant pair</td>
<td>28 March</td>
<td>3.2</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>RB:77-78 Subordinates</td>
<td>25 April</td>
<td>3.3</td>
<td>428</td>
<td></td>
</tr>
<tr>
<td>RB:78-79 Dominant pair</td>
<td>24 March</td>
<td>2.9</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>RB:78-79 Subordinates</td>
<td>17 April</td>
<td>3.1</td>
<td>519</td>
<td></td>
</tr>
</tbody>
</table>

*Includes pairs consisting of one formerly subordinate individual (see text).

Does not include males which remained unpaired.

Calculated by converting dates to day-number of year, e.g., 2 Feb. = day # 33.

Samson and Lewis (1979) reported that 3–4 male titmice from one flock established territories within their flock’s range. Presumably these birds included an alpha male and subordinates. We cannot account for the differences in the titmice’s spring activity in our study and that of Samson and Lewis (1979).

Winter flocks of the various species in Paridae have been categorized into two groups by Saitou (1978). The first group is made up of species that form conspecific flocks, often of more than two individuals, and regularly participate in mixed-species flocks. Great Tits (*P. major*), Black-capped Chickadees, and Carolina Chickadees (*P. carolinensis*) are species belonging to this group. The second group consists of species such as Marsh Tits (*P. palustris*), Plain Titmice (*P. inornatus*), and Willow Tits (*P. montanus*). These species spend the winter in pairs, rarely form larger conspecific groups, and participate in mixed flocks when they are present within a pair’s territory. Saitou (1978) tentatively classified Tufted Titmice as a species of the first category. Our data indicate that Tufted Titmice share characteristics of both groups but may be more appropriately assigned to the second group. Six of the 14 flocks in our study were comprised of a single pair whose participation in mixed-species flocks was limited.
In recent years there has been considerable study devoted to determining the advantages of flocking over solitary existence during the non-breeding period. Greater foraging efficiency and/or increased protection from predators are general factors that are most often suggested as advantages of flocking (Krebs et al. 1972, Morse 1977, Rubenstein et al. 1977). Other, more specific, analyses have considered flock-size, composition and movements in relation to rates of inter- and intra-specific aggression (Barash 1974, Caraco 1980) and weather (Grubb 1975).

All of the above advantages and considerations are likely relevant to titmouse flocks; however, there are certain aspects of the flocks that are also related to events in the breeding season. For example, titmouse dominance hierarchy may serve all flock members by reducing intra-specific aggression during a time of energetic stress (Smith 1976). Dominant birds clearly are afforded an additional advantage the following spring by being able to breed before subordinate conspecifics in habitats where nest-sites may be limited (Hardin and Evans 1977) and on areas with which they are familiar.

The asynchrony in initiation of breeding between dominant and subordinate birds was likely due to alpha males' intolerance of other titmice, especially males. This behavior typically resulted in the alpha males and females having sole ownership of the flock range after the groups broke up. Thus, subordinate birds were forced to seek undefended areas. We observed subordinate birds travelling over relatively long distances during this period (Table 3). Some subordinates eventually gained access to a part of their former flock's winter range. A female that is forced to search for a breeding territory and/or a mate may expend energy that might otherwise be allocated to reproduction. Other studies of parids have documented that birds breeding early have greater reproductive success than those that breed relatively late (Perrins 1979).

**SUMMARY**

Fourteen winter flocks of Tufted Titmice (*Parus bicolor*) were studied in central Missouri from 1977 to 1979. The flocks formed during late September and early October. Flock size ranged from 2-5 individuals (\( \bar{x} = 2.9 \)). Males were more common than females among adults and juveniles.

Six of the flocks consisted of one adult male and one female. The flock structure was generally stable throughout the flocking period. Seven birds disappeared from the flocks during the two field seasons. The intra-flock dominance hierarchies were linearly peck-right. Males were dominant over females. Dominance within a sex appeared to be determined by seniority on the flock territory. Titmice typically travelled alone, in pairs, or in groups of three. Certain pairs preferred specific portions of their flock's range for winter activity. The flocks disbanded during late February and March. In 12 of 14 cases the dominant males and females of the flocks proved to be paired and established breeding territories within the winter flock ranges. Consistently, these pairs were the first or only titmice to breed on the
flock ranges. The asynchrony in the initiation of breeding between the dominant and subordinate birds may be an important aspect of the titmice’s winter flock dominance hierarchy.

ACKNOWLEDGMENTS

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FOOD SUPPLY AND THE OCCURRENCE OF BROOD REDUCTION IN SWAINSON'S HAWK

MARC J. BECHARD

The adaptive significance of hatching asynchrony has received considerable attention over the past two decades (Ingram 1959; Ricklefs 1965; Lack 1966; Skutch 1967; Bryant 1975; Proctor 1975; Newton 1977, 1979). Arguments, based primarily on Lack’s (1966) food-limited hypothesis, suggest that it gives species dependent on irregular or unpredictable food sources a means of adjusting reproductive effort to prevailing food supplies. The consensus is that hatching asynchrony gives older, more developed nestlings a survival advantage during periods of limited food by increasing the chances they will eliminate late-hatched chicks through starvation or fratricide and thereby prevent their own demise. The hypothesis has been criticized for its apparent wastefulness (Ricklefs 1968, Hussel 1972, Proctor 1975, O’Connor 1977), but if one considers the inclusive fitness of all nestlings, it may have adaptive value (O’Connor 1978, Stinson 1979).

Food-related incidences of brood reduction supporting the theory have been reported in a number of species (Ricklefs 1965, Nisbet and Cohen 1975, Parsons 1975, Proctor 1975). Although brood reduction has been observed at many raptor nests (Ingram 1959, 1962; Heintzelman 1966; Clevenger and Roest 1974; Meyburg 1974; Stinson 1979), data linking its occurrence with limited food supply are lacking. Possible and confirmed records of fratricide and cannibalism have been reported at nests of Swainson’s Hawk (Buteo swainsoni) (Pilz 1976; Parker 1976, 1979; Pilz and Seibert 1978; Newton 1979), for example, but none have been linked with food supply. Here, I use nestling weight as an index of nestling food supply to demonstrate the relationship between limited food availability and the occurrence of brood reduction in this species.

STUDY AREA AND METHODS

The study was conducted in southeastern Washington in an approximately 4200-km² area of Whitman and Garfield counties (Bechard 1980). The native habitat once consisted of shrub-steppe vegetation (Daubenmire 1970). Because of agriculture, only small patches of native habitat remain in creek bottoms and on steep terrain, and large expanses of cropland planted in wheat, peas, barley, and lentils now dominate the landscape.

The climate is characterized by moderately cold, wet winters and hot, dry summers. Mean temperature for the coldest month (January) ranges from −5.5–1.5°C while the hottest month (August) ranges from 18.5–24.5°C. Rainfall averages from 35.5–63.5 cm per year. During the study, precipitation was average in 1978 and 1979, but a drought occurred in 1977 when
monthly precipitation was well below average from January through April. The drought reduced vegetative cover in cropland and yields were as much as 50% below average.

The study area was searched from 1976 through 1979 for Swainson’s Hawk nests. Information concerning nest-sites was also obtained from a survey of local Audubon Society members and Washington State Department of Game personnel. Nests were considered active if a pair of Swainson’s Hawks were present and if there was evidence of nest-building activity. Each nest was classified as being in either grazed or cultivated habitat by using the dominant form of land use in surrounding habitats.

Three weeks after the start of incubation, I determined clutch-size using a mirror attached to a telescoping 12-m aluminum pole. After hatching was completed, nest trees were climbed every 5 days to determine brood-size at hatching, nestling mortality, and nestling weight gain. Nestling weight was obtained to the nearest 5 g using a 1000 g Pesola spring balance.

Forty-one of the 87 nestlings studied were found either while hatching or obviously within their first 24 h of life; these were therefore of known age. Other nestlings were aged by back-dating from the average hatching interval of 2 days (Bent 1961; Parker 1976; Pilz and Seibert 1978; Fitzner 1980; Bechard, unpubl.) using known-age nestlings as references. I considered this aging method to be accurate within 1 day. To identify young in nests, I used fingernail polish to mark the talons of very young chicks, later substituting individually numbered U.S. Fish and Wildlife Service leg bands.

To determine nestling diets, castings and prey remains were noted and/or collected from each nest. Remains were identified using skull fragments, lower jaws, claws, hair, and feathers. Relative percent frequency estimates were calculated for each prey taxon based on the total number of individuals identified (Curtis and McIntosh 1950).

RESULTS

I observed 87 nest attempts at 44 Swainson’s Hawk nests during the 4-year study and obtained data for an additional nine nests observed in 1975 (Fitzner 1977). Some of the nests were in habitats grazed by livestock, but most occurred in areas of crop cultivation. Over 75% were in black locust (Robinia pseudoacacia) at an average height of 9.9 ± 4.7 m (range 3.5–27.1 m). Nests contained an average of 2.66 ± 0.47 eggs (range 2.37–2.9, N = 33) (Table 1). Ninety-three percent of the eggs hatched to produce broods averaging 2.36 ± 0.11 (range 2.0–3.15) nestlings per nest. Fledging success averaged 1.11 ± 0.06 (range 0.67–2.21) young per active nest. Compared to averages of 1.5–2.0 young per nest reported by Olendorff (1973), Smith and Murphy (1973), Keir (1976), Dunkle (1977), and Fitzner (1977), my data indicated a relatively low level of nesting success.

Estimates of clutch-size, brood-size, and fledging success varied from year-to-year. Kruskal-Wallis 1-way ANOVA, however, showed that only estimates of fledging success varied significantly ($\chi^2 = 4.82, df = 4, P \leq 0.05$). All three estimates also tended to be smaller in cultivated than grazed habitats, but only the differences in fledging success were significant (Wilcoxon two-sample test, $U_s = 1105$, $N_1 = 56, N_2 = 31, P \leq 0.05$).

Decreased fledging success in 1978 and 1979 resulted from high nestling mortality, particularly in cultivated habitats (Fig. 1). Mortality occurred
### Table 1

**Productivity of Swainson’s Hawk Nests in Grazed and Cultivated Habitats in Southeastern Washington**

<table>
<thead>
<tr>
<th>Year</th>
<th>Habitat</th>
<th>Clutch-size (Nest)</th>
<th>Brood-size (Nest)</th>
<th>No. young per active nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>Overall</td>
<td>—</td>
<td>—</td>
<td>0.67 (9)&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>1976</td>
<td>Cultivated</td>
<td>—</td>
<td>2.0 (2)</td>
<td>0.66 (3)&lt;sup&gt;c,d&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Grazed</td>
<td>—</td>
<td>2.0 (2)</td>
<td>1.0 (2)&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>—</td>
<td>2.0 (4)</td>
<td>0.83 ± 0.20 (5)&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>1977</td>
<td>Cultivated</td>
<td>2.72 ± 0.13 (11)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.54 ± 0.12 (11)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.41 ± 0.12 (12)</td>
</tr>
<tr>
<td></td>
<td>Grazed</td>
<td>3.15 ± 0.17 (6)</td>
<td>3.15 ± 0.17 (6)</td>
<td>2.00 ± 0.24 (7)</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>2.90 ± 0.11 (17)</td>
<td>2.76 ± 0.14 (17)</td>
<td>2.21 ± 0.12 (19)</td>
</tr>
<tr>
<td>1978</td>
<td>Cultivated</td>
<td>2.30 ± 0.17 (9)</td>
<td>2.11 ± 0.11 (9)</td>
<td>0.63 ± 0.18 (19)</td>
</tr>
<tr>
<td></td>
<td>Grazed</td>
<td>2.42 ± 0.19 (7)</td>
<td>2.28 ± 0.19 (7)</td>
<td>0.88 ± 0.20 (9)</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>2.37 ± 0.12 (16)</td>
<td>2.18 ± 0.10 (16)</td>
<td>0.75 ± 0.16 (28)</td>
</tr>
<tr>
<td>1979</td>
<td>Cultivated</td>
<td>2.57 ± 0.13 (14)</td>
<td>2.35 ± 0.13 (14)</td>
<td>0.95 ± 0.11 (22)</td>
</tr>
<tr>
<td></td>
<td>Grazed</td>
<td>3.00 ± 0.07 (7)</td>
<td>2.85 ± 0.11 (7)</td>
<td>1.30 ± 0.20 (13)</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>2.71 ± 0.10 (21)</td>
<td>2.52 ± 0.11 (21)</td>
<td>1.12 ± 0.15 (35)</td>
</tr>
</tbody>
</table>

<sup>a</sup> Taken from Fitzner (1977).
<sup>b</sup> Number of nests observed.
<sup>c</sup> Annual means significantly different (Kruskal-Wallis 1-way ANOVA, P < 0.05).
<sup>d</sup> Means in grazed and cultivated habitats significantly different (Wilcoxon two-sample test, P < 0.05).

When nestlings were from 15–30 days of age and was most frequent when they were between 20 and 25 days old. I could not determine if deaths resulted from starvation or fratricide at all nests, but the bloody heads of live birds indicated that fratricide may be a common cause of death. Partially eaten young were found in 10 of 16 nests in 1978 and in 15 of 26 nests in 1979. In all of these cases it was the youngest nestling that died; at two of four nests in 1978 and 4 of 10 nests in 1979 that started with broods of three young, further brood reduction occurred when the second youngest nestling died. Only four incidences of brood reduction occurred in 1977. All involved the deaths of youngest nestlings and all but one took place in cultivated habitats.

Diets of nestling hawks consisted primarily of small rodents (Table 2). Northern pocket gophers were the most frequently consumed prey, especially in grazed habitats. In cultivated habitats, gophers were the most common dietary constituent in 1978, but in 1977 and 1979 deer mice and voles were more common dietary items. Columbian ground squirrels and birds were consumed but they remained of minor dietary importance throughout the study.

Assuming that the survival of nestling Swainson’s Hawks would be high-
Fig. 1. Nestling survival in grazed and cultivated habitats of southeastern Washington during 1977, 1978, and 1979; same sizes as indicated in Fig. 2.

Nestling survival in grazed and cultivated habitats of southeastern Washington during 1977, 1978, and 1979; same sizes as indicated in Fig. 2.

ly correlated with food supply, I weighed nestlings to obtain an index of the amount of food fed to them (Fig. 2). Twenty-nine, 21, and 37 nestlings were weighed at the start of brood periods in 1977, 1978, and 1979, respectively. Nestling weights were similar in grazed and cultivated habitats in 1977 when fledging success was high, but when success was low in 1978 and 1979, weights were lower in cultivated habitats. Decreased weight was
The diets of nestling Swainson’s Hawks in grazed and cultivated habitats of southeastern Washington, 1977–1979

<table>
<thead>
<tr>
<th>Frey species</th>
<th>Grazed habitat % frequency&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Cultivated habitat % frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small mammals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern pocket gopher (Thomomys talpoides)</td>
<td>86</td>
<td>67</td>
</tr>
<tr>
<td>Mountain vole (Microtus montanus)</td>
<td>46</td>
<td>72</td>
</tr>
<tr>
<td>Deer mouse (Peromyscus maniculatus)</td>
<td>19</td>
<td>11</td>
</tr>
<tr>
<td>Columbian ground squirrel (Citellus colubrianus)</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>Desert cotton-tail rabbit (Sylvilagus audubonii)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Long-tailed weasel (Mustella frenata)</td>
<td>4</td>
<td>—</td>
</tr>
<tr>
<td>Birds</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ring-necked Pheasant (Phasianus colchicus)</td>
<td>—</td>
<td>72</td>
</tr>
<tr>
<td>Hungarian Partridge (Perdix perdix)</td>
<td>25</td>
<td>—</td>
</tr>
<tr>
<td>Black-billed Magpie (Pica pica)</td>
<td>75</td>
<td>14</td>
</tr>
<tr>
<td>Western Meadowlark (Sturnella neglecta)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Horned Lark (Eremophila alpestris)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>House Sparrow (Passer domesticus)</td>
<td>—</td>
<td>14</td>
</tr>
<tr>
<td>Eurasian Starling (Sturnus vulgaris)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Short-eared Owl (Asio flammeus)</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>Reptiles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gopher snake (Pituophis melanoleucus)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Insects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grasshopper (Melanoplus sp.)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
<sup>a</sup> Percent frequency based on the total number of individuals identified.

particularly evident when nestlings ranged from 15–25 days old, the period when mortality was highest. Comparison of the decrease in survival with the decrease in nestling weight yielded a significant Spearman Rank correlation \(r_s = 0.57, N = 21, P \leq 0.01\) and indicated that food supply affected nestling survival in cultivated habitats.

Sibling weights were similar when survival was high, but during years of low nestling survival, younger siblings weighed less than their older nest mates did at the same age (Fig. 3). I compared the decrease in survival of youngest siblings with the difference in their own weight and the weight of their oldest siblings at the same age. Again, I obtained a highly significant correlation \(r_s = 0.81, N = 21, P \leq 0.01\) which indicated that competition in nests decreased the food available to younger nestlings and lowered their chances of survival.
Fig. 2. Mean weights (±1 SE) of nestling Swainson's Hawks in grazed and cultivated habitats of southeastern Washington during 1977, 1978, and 1979; nestling weight based on the number of observations given in parentheses.

DISCUSSION

Nestling weight has frequently been used as an index of food supply (Owen 1960; Ricklefs 1965; Blaxter 1968; Southern 1970; Seel 1970; Perrins 1970; Spaans 1971; Dunn 1973, 1975; Bryant 1975). If this is valid, the nestling weight data I report support the food-limited hypothesis for hatching asynchrony and brood reduction in Swainson's Hawk. The cor-
Fig. 3. Mean weights (±1 SE) of youngest and oldest nestlings of Swainson's Hawks nesting in southeastern Washington during 1977, 1978, and 1979; nestling weights based on the number of observations given in parentheses.

A relation linking poor nestling survival with decreased weight suggests that limited food supplies increase the incidence of brood reduction. Also, the correlation between poor survival of youngest nestlings and the difference between sibling weights indicates that hatching asynchrony gives older nestlings a survival advantage by increasing their portion of the food supply. Weight differences between youngest and oldest nestlings of Great Reed Warblers (Acrocephalus arundinaceus), House Martins (Delichon ur-
bica), and House Sparrows (Passer domesticus) have also been reported and related to food supply (Seel 1970, Dyrcz 1974, Bryant 1978). Proctor (1975) has found weight differences between siblings of South Polar Skuas (Catharacta maccormicki) and that increases in this difference resulted in poor survival of younger nestlings because of attacks from their larger, hungrier, older siblings. Weight differences I observed between nestling Swainson’s Hawks were greatest at 25 days of age and coincided with the period when brood reduction was most common. At 25 days of age, oldest nestlings had reached approximately 75% of their adult weight, a period in development when metabolic needs reach a maximum (Ricklefs 1974). The occurrence of fratricide at this time indicated that oldest nestlings were not being fed enough food and that hunger and competition resulted in the deaths of younger nest-mates.

Vegetative cover and weather affect the hunting success of many raptors including Swainson’s Hawks (Craighead and Craighead 1956; Southern and Lowe 1968; Wakeley 1978; Bechard 1980, 1982; Stinson 1980). In view of this, one would assume that it is difficult for these birds to “predict” food supply during a breeding season and that adjustments in reproductive effort would out of necessity be made via hatching asynchrony and brood reduction. My observations support this hypothesis. Apparently, unable to adjust clutch-size to annual changes in prey availability, Swainson’s Hawks laid the same number of eggs each year. By hatching them asynchronously, however, adults insured that, if food became critical, brood reduction would adjust reproductive effort by eliminating younger nestlings. In so doing, they prevented the starvation of all nestlings and total failure of the nesting attempt.

SUMMARY

Clutch-size, brood-size, and fledging success were observed at 96 Swainson’s Hawk (Buteo swainsoni) nests in both grazed and cultivated habitats in southeastern Washington. Except in 1977, nests in cultivated habitats fledged fewer young. Decreased fledging success resulted from high mortality of youngest and next youngest nestlings. Using nestling weight as an index of food supply, decreases in nestling weight and increases in weight discrepancies between youngest and oldest nestlings in cultivated habitats indicated that a dearth of food increased the incidence of brood reduction. These data supported the food-limited hypothesis for the adaptive significance of hatching asynchrony in this species.

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LITERATURE CITED


PRODUCTIVITY OF OSPREYS IN THE GULF OF CALIFORNIA

DEBRA S. JUDGE

The decrease in numbers of Ospreys (*Pandion haliaetus*) that coincided with the use of chlorinated hydrocarbon pesticides aroused interest in determining their population sizes and productivity in North America (e.g., Henny and Wight 1969, Henny and Ogden 1970, Henny 1975, Henny and Noltemeier 1975, Wiemeyer et al. 1975, Roberts and Lind 1977). Many populations along the east coast of the United States have been monitored for the past 15 years (Henny and Ogden 1970). These populations consist of migratory Ospreys that spend the winter in Central and South America (Henny and Van Velzen 1972).

Within North America, non-migratory populations of Ospreys are currently found in southern Florida (Ogden 1975, 1977) and in Baja California, along the coast of Sonora, and throughout the Gulf of California islands, Mexico (Friedman et al. 1950). Prior to 1930, the Baja California population extended into southern California (Kenyon 1947, Jones and Diamond 1976). A recent aerial survey of the Baja California and Gulf of California regions resulted in an estimated population of 810 ± 55 pairs of Ospreys (Henny and Anderson 1979). This paper reports the results of an investigation of the phenology of reproduction and productivity of a portion of this population during 1977 and 1978.

STUDY AREA AND METHODS

The study area encompassed a cluster of 16 small islands in the Bahia de los Angeles (28°57'N, 113°33'W) on the eastern coastline of Baja California Norte, Mexico. In 1977 and 1978, Ospreys nested on 11 of these islands at the tops of razorback cliffs and rock pinnacles or on rock out-crops that characterized the shorelines. Plant life comprised sparse Sonoran Desert vegetation (Shreve and Wiggins 1964, Coyle and Roberts 1975) and was physiognomically dominated by Cactaceae.

Fieldwork was conducted between 19 January and 7 June and 20 August–16 September 1977, and between 13 January and 6 June 1978. Censuses of Ospreys and their nests were undertaken at approximately 4–5-week intervals. Censuses were conducted by boat along shorelines on clear and calm days when conditions were optimal for locating Ospreys and climbing to their nests. Five breeding season censuses were made in 1977 and four in 1978. Each census took approximately 2 days. Censuses comprised the minimal number of times that any nest was visited; approximately 40% of occupied nests were visited at least once in 10 days in the course of intensive behavioral observations.

Occupancy of nest and stage of the breeding cycle were determined by observations of nest contents and the behavior of adult Ospreys in attendance. During each census, sizes of clutches and/or broods, nest defense by adults, nest construction and size, and the presence and type of food remains were recorded for each accessible nest. Hatching success,
mortality of nestlings, and fledging success were calculated from data obtained during all visits. In some cases, hatching dates could be back-dated for nestlings that were less than 1 week of age by comparison of developmental characteristics with known age nestlings.

Some adult Ospreys could be individually recognized by distinctive head plumage patterns. United States Fish and Wildlife Service bands placed on them as nestlings prior to this study by D. W. Anderson (N = 3), by colored polyvinyl chloride, wrap-around leg bands applied during this study (N = 3), or by combinations thereof. The sex of each adult Osprey was determined by size, breast coloration (Macnamara 1977), and behavior. Young Ospreys were initially identified by ink-marking their tarses and subsequently by individual colored leg band combinations.

Standard Chi-square analyses of a 2 × 2 contingency table (uncorrected \( \chi^2 \), see Remington and Schork 1970:271) were used to compare proportions except in cases of small sample sizes wherein I used Fisher’s Exact Probability test (Sokal and Rohlf 1969:595). A series of “t-tests for the approximate equality of means assuming unequal variances” (Sokal and Rohlf 1969:374) were used to compare mean clutch-sizes of Ospreys for geographical regions of North America.

RESULTS AND DISCUSSION

**Nest structures.**—Sixty-five and 68 nests were located in 1977 and 1978, respectively. Structural elements of nests included driftwood, woody parts of cardon cactus (*Pachycereus pringlei*), ocotillo (*Fouquieria* sp.), and skulls and long-bones of Brown Pelicans (*Pelecanus occidentalis*). Aquatic vegetation, terrestrial vines, and beach-cast debris were used in both construction and lining of nests.

**Nest use and persistence.**—Most nests within the study area were known from previous censuses to be at least 7 years old at the onset of this study (D. W. Anderson, pers. comm.). Nests may be used for many consecutive years or may be abandoned for 1 or more years (D. W. Anderson, unpubl.). Nests are durable and survive high winds and occasional storms characteristic of the Gulf of California; thus, large numbers of unoccupied nests do not necessarily indicate recent, overall declines in the size of the breeding population in this area.

There were nine nest-site changes between 1977 and 1978. Three of the nine changes involved newly constructed nest structures, the remaining six were present but unused in 1977. All nest changes were associated with the abandonment of a nearby nest. Each of the changes (N = 3 pairs) wherein the adult Ospreys were recognizable involved a new pair member in 1978 (at one there was a new male and at each of the other two there was a new female). Seven recognizable pairs used the same nests in each of the 2 years. This suggests that nest-site tenacity and pair-bond maintenance are in some way positively related. Fernandez and Fernandez (1977) concluded that Ospreys they observed were faithful to territory, nest, and mate, in that order.

Forty-eight (1977, N = 65)—51% (1978, N = 68) of the nests were either
unused or were used as "alternate nests" (Postupalsky 1977) for feeding and as perches by pairs of Osprey that laid their eggs in, or spent most of their time at, another nest. Alternate nests were used throughout the breeding season by both successful and unsuccessful breeders.

*Residency and nest use in the non-breeding season.*—Censuses during the post-breeding season in late August and early September 1977 revealed approximately 12 Ospreys. These Ospreys perched and fed solitarily (not as members of pairs), were not closely associated with nest structures, and exhibited only sporadic alarm vocalizations when I visited nests. Intraspecific social interactions among Ospreys that were initiated during the breeding season by vocal responses to my nest visits facilitated observation; thus, the 12 Ospreys I counted can be assumed to be the minimum number in residence.

*Breeding chronology.*—Breeding chronology of Ospreys in the Gulf of California was characterized by a high degree of asynchrony. The onset of egg-laying ranged approximately 9–10 weeks from early January to early March during both years (Table 1). The mean incubation period (first-egg date to first-hatch date) for six clutches was 38.3 ± 3.2 days. Minimum lengths of incubation for 10 additional clutches ranged from 32–42 days ($\bar{x} = 37.9 \pm 3.1$). Kenyon (1947) and Jehl (1977) reported that all stages of the breeding chronology could be found concurrently in Ospreys nesting on the west coast of Baja California during April and March, respectively. Resident Ospreys in southern Florida exhibit a similarly protracted breeding season (Ogden 1977). In more northern, migratory populations all eggs are usually laid within a 3-week period (Ames 1964, Garber 1972, Kennedy 1977, Parnell and Walton 1977, Prevost et al. 1978).

Hatching began in early February in 1977 and in late February in 1978, and extended through late April in both years (8–9 weeks) (Table 1). Mean nestling period (hatch to first sustained flight) was 62.5 ± 4.9 days for 10 broods. Minimum nestling periods for six additional broods ranged from 52–76 days. The variation in incubation and in nestling periods is responsible, in part, for the changing distribution of numbers of nests with young hatching and fledging over the season in Table 1. Fledging first occurred during early April in 1977 and in late April in 1978. In both years all nestlings fledged by the second week in June (7–9 weeks).

*Breeding success.*—Pairs occupied 52% of the nest structures in 1977 and 49% in 1978 as primary nest-sites (nests in which pairs spent most of their time and/or laid eggs) (Table 2). Solitary Ospreys with the dark dorsal plumage characteristic of all but first-year birds (Bent 1937:365) attended at least three additional nests during both years. In 1977, females in 94% of the pairs laid eggs, 75% of these clutches subsequently resulted in at least one nestling, and 66% of these pairs successfully fledged at least one
Table 1
Breeding Chronology of Ospreys in Bahia de los Angeles: Number of Nests (%) in Which Laying (L), Hatching (H), and Fledging (F) Began During Each 2-Week Period

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1-15 Jan.</td>
<td>8 (27)</td>
<td>5 (19)</td>
<td>16-31 Jan.</td>
<td>7 (23)</td>
<td>9 (33)</td>
<td></td>
</tr>
<tr>
<td>1-14 Feb.</td>
<td>8 (27)</td>
<td>7 (26)</td>
<td>15-28 Feb.</td>
<td>4 (13)</td>
<td>5 (19)</td>
<td>2 (07)</td>
</tr>
<tr>
<td>1-15 Mar.</td>
<td>3 (10)</td>
<td>1 (04)</td>
<td>16-31 Mar.</td>
<td>5 (17)</td>
<td>3 (11)</td>
<td></td>
</tr>
<tr>
<td>1-15 Apr.</td>
<td>1 (03)</td>
<td>2 (07)</td>
<td>16-30 Apr.</td>
<td>1 (03)</td>
<td>4 (13)</td>
<td>1 (04)</td>
</tr>
<tr>
<td>1-15 May</td>
<td>5 (17)</td>
<td>5 (19)</td>
<td>16-31 May</td>
<td>6 (20)</td>
<td>3 (11)</td>
<td></td>
</tr>
<tr>
<td>1-7 Jun.</td>
<td>2 (07)</td>
<td>4 (15)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

young (Table 2). In 1978, females in 85% of the pairs occupying nests laid eggs, 71% of these yielded at least one nestling, and 50% of these active pairs fledged at least one young (Table 2).

Clutch-size comparisons. — There was no statistically significant association between clutch timing and clutch-size in either 1977 or 1978 (Fisher Exact P = 0.10 and 0.25 for 1977 and 1978, respectively). Combining the data for the 2 years and comparing early vs late clutches via a χ² test for association indicated that more large (three-egg) clutches were laid early in the laying period (χ² = 4.66, df = 1, P < 0.05) (Table 3).

The mean clutch-size for active pairs was not significantly different between 1977 and 1978 (t = 1.58, df = 50, P > 0.10). The 2-year mean clutch-size of active pairs (pairs that laid at least one egg) was 2.8 ± 0.08.

Historic and geographic comparisons. — There was no significant difference between the mean clutch-size of active pairs during this study and the mean clutch-size of egg sets collected in Baja California and southern California prior to 1947 (the year after which pesticide related egg shell thinning occurred in some species in the United States, Hickey and Anderson 1968) (Table 4). Mean clutch-size of Ospreys from Baja California (pre-1947 and current) were significantly smaller than the means of Osprey clutches taken from as far south as South Carolina on the east coast. The pre-1947 Baja California mean was also significantly smaller than the mean for pre-1947 Georgia and Florida breeding Ospreys: how-
### Table 2
#### SUMMARY OF OSPREY PRODUCTIVITY

<table>
<thead>
<tr>
<th></th>
<th>1977</th>
<th>1978</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N (%), ±SE</td>
<td>N (%), ±SE</td>
</tr>
<tr>
<td>Nest structures</td>
<td>65 (100)</td>
<td>68 (100)</td>
</tr>
<tr>
<td>No. nests occupied by single adults</td>
<td>3 (05)</td>
<td>3 (04)</td>
</tr>
<tr>
<td>No. nests attempts</td>
<td>34 (52)</td>
<td>33 (49)</td>
</tr>
<tr>
<td>No. active pairs</td>
<td>32</td>
<td>28</td>
</tr>
<tr>
<td>Average clutch-size/active pair</td>
<td>30 2.7 ± 0.1</td>
<td>25 2.9 ± 0.1</td>
</tr>
<tr>
<td>No. of nests with nestlings</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>No. of nests with fledglings</td>
<td>21</td>
<td>14</td>
</tr>
<tr>
<td>No. fledged/nest attempt</td>
<td>34 0.6</td>
<td>33 0.4</td>
</tr>
<tr>
<td>No. fledged/active nest</td>
<td>32 1.0</td>
<td>28 0.9</td>
</tr>
<tr>
<td>No. fledged/productive nest</td>
<td>21 1.5</td>
<td>14 1.9</td>
</tr>
<tr>
<td>Hatching success (#hatched/#laid)</td>
<td>49/76 0.6</td>
<td>41/66 0.6</td>
</tr>
<tr>
<td>Fledging success (fledged/nestlings)</td>
<td>32/49 0.7</td>
<td>26/41 0.6</td>
</tr>
<tr>
<td>Total young fledged</td>
<td>32</td>
<td>26</td>
</tr>
</tbody>
</table>

*a* Nest attempts are number of pairs occupying nests.

*b* Sample sizes for some calculations varied due to differences in accessibility of nests in various stages.

*c* Active pairs are those that laid eggs.

*d* Productive pairs (nests) are those from which at least one young fledged.

---

...ever, the Bahia de los Angeles mean was not significantly different from the pre-1947 Georgia and Florida mean (Table 4). This minor difference may be due to the variety of data collection methods (museum egg sets vs more accurate field observations). The population in southern Florida is the only other North American population that is non-migratory (Ogden 1977). This may indicate that a relatively low clutch-size is related to ecological and life-history characteristics associated with a non-migratory habit. Temperature regimes, annual patterns of food availability, etc., allow year-round residency in the area of the Gulf of California. This residency could, in turn, result in adults investing energy into young for a longer portion of the year (unpubl.) which, in conjunction with the lack of a long migration in the natal year, might result in increased survivorship of juveniles and subsequently might allow lower clutch-sizes than those selected for in migratory populations with high first year mortality (Henny and Wight 1969).

**Hatching success.—**Hatching success (number of nestlings/number of eggs) was approximately equal for the 2 years of this study (Table 2). In 1977, a lower percentage of eggs in clutches of two eggs hatched (38%) than in clutches of three (68%) ($\chi^2 = 5.16$, df = 1, $P < 0.025$; Table 5). Percents of eggs hatching were approximately equal for clutches of two
Table 3
Clutch-sizes of Ospreys in Relation to Time of Clutch Initiation

<table>
<thead>
<tr>
<th>Timing</th>
<th>N</th>
<th>2 eggs (%)</th>
<th>3 eggs (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>22</td>
<td>4 (18)</td>
<td>18 (82)</td>
</tr>
<tr>
<td>Late</td>
<td>8</td>
<td>4 (50)</td>
<td>4 (50)</td>
</tr>
<tr>
<td>Total</td>
<td>30</td>
<td>8 (27)</td>
<td>22 (73)</td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>18</td>
<td>2 (11)</td>
<td>16 (89)</td>
</tr>
<tr>
<td>Late</td>
<td>6</td>
<td>2 (33)</td>
<td>4 (67)</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>4 (17)</td>
<td>20 (83)</td>
</tr>
<tr>
<td>Both years</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>40</td>
<td>6 (15)</td>
<td>34 (85)</td>
</tr>
<tr>
<td>Late</td>
<td>14</td>
<td>6 (43)</td>
<td>8 (57)</td>
</tr>
<tr>
<td>Total</td>
<td>54</td>
<td>12 (22)</td>
<td>42 (78)</td>
</tr>
</tbody>
</table>

* Early and late denotes first or second half of laying period.

and three in 1978 (62% and 57%, respectively) ($\chi^2 = 0.098$, df = 1, NS; Table 5). Comparison of the hatching success (hatched vs not-hatched) of early vs late clutches of three revealed a significantly higher success in early 1977 clutches ($\chi^2 = 4.88$, df = 1, $P < 0.05$), but no difference in early vs late 1978 clutches of three ($\chi^2 = 1.78$, df = 1, NS; Table 6).

**Fledging success.**—The number of young fledged per egg was the same for the 2 years (Table 2); however, relationships between the time of clutch initiation and success for three-egg clutches to fledging differed (Table 6). During the 1977 season, clutches of three initiated early in the season yielded more fledglings than did those initiated later in the season ($\chi^2 = 6.06$, df = 1, $P < 0.05$). In 1978, there was no significant difference in the success of production associated with timing ($\chi^2 = 0.23$, df = 1, NS). Combining data from both years showed a significant, overall association of fledging success with early initiation of laying ($\chi^2 = 4.1$, df = 1, $P < 0.05$). Fledging success does not appear to be associated with initial clutch-size ($\chi^2 = 0.62$, df = 1, NS). In this study, the number of young fledged per active nest is similar to mean numbers of young reported fledging per occupied nest in many prior studies in North America (see Henny 1975 for review). The reason for this is not clear; however, it may be explained if sexually mature, non-migratory Ospreys are more likely to remain in a breeding area without attempting to reproduce than are more northern-breeding, migratory, adult Ospreys.

In neither of the 2 years was there a significant difference in the success of raising nestlings to fledging age among broods from early vs late breed-


Table 4

Geographic Comparison of Mean Clutch-sizes as Determined from Pre-1947 Egg Sets of Museums in North America and for Recent Studies in the Western United States

<table>
<thead>
<tr>
<th>Region</th>
<th>N</th>
<th>( \bar{x} \pm SE )</th>
<th>Differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>N.E. North America (ME, NH, VT, NB, NS)</td>
<td>43</td>
<td>3.02 ± 0.04</td>
<td>A</td>
</tr>
<tr>
<td>E. North America (CT, MA, NY)</td>
<td>685</td>
<td>3.09 ± 0.02</td>
<td>A</td>
</tr>
<tr>
<td>Atlantic Seaboard (DE, MD, NC, SC, VA)</td>
<td>299</td>
<td>3.23 ± 0.03</td>
<td>B</td>
</tr>
<tr>
<td>S.E. North America (GA, FL)</td>
<td>57</td>
<td>2.84 ± 0.07</td>
<td>C</td>
</tr>
<tr>
<td>S.W. North America (S. CA, BC)</td>
<td>76</td>
<td>2.67 ± 0.07</td>
<td>D</td>
</tr>
<tr>
<td>Bahia de los Angeles (1977, 1978)</td>
<td>51</td>
<td>2.78 ± 0.07</td>
<td>C D</td>
</tr>
<tr>
<td>N. California (Garber 1972)</td>
<td>80</td>
<td>2.77 ± 0.08</td>
<td>C D</td>
</tr>
</tbody>
</table>

\(a\) Museum data provided by D. W. Anderson.

\(b\) Means for geographical regions that are not significantly different (\(P > 0.05\)) share the same letter(s) and those that are significantly different have different letters.

\(c\) ME = Maine, NH = New Hampshire, VT = Vermont; NB = New Brunswick, NS = Nova Scotia, Canada.

\(d\) CT = Connecticut, MA = Massachusetts, NY = New York.

\(e\) DE = Delaware, MD = Maryland, NC = North Carolina, SC = South Carolina, VA = Virginia.

\(f\) GA = Georgia, FL = Florida.

\(g\) S. CA = Southern California; BC = Baja California, Mexico.

ers (fledged vs not fledged 1977, \(\chi^2 = 2.3, \text{df} = 1, \text{NS and 1978 Fisher Exact } P = 0.38\) (Table 6). Combining data from both years and testing for differences in the proportion of nestlings that fledged also revealed no significant difference (\(\chi^2 = 0.57, \text{df} = 1, \text{NS}\)). Thus, during this 2-year study, the advantage of laying early in the season occurred prior to hatching rather than being related to the chronological period in which nestlings were present.

In 1977, nestlings in broods of two were more successful in fledging (not less than 86%) than nestlings in broods of three (37%) (Fisher Exact \(P = 0.0007, \text{Table 7}\)). In 1978, broods of two and three exhibited fledging successes of 56 and 67%, respectively. Overall, significantly more nestlings in broods of two young fledged (72.5%) than did those in broods of three (51%) (\(\chi^2 = 4.08, \text{df} = 1, P < 0.05\)). In 1977, an average of 1.5 young fledged per productive nest whereas, in 1978, an average of 1.9 young fledged. Thus, 33% fewer productive nests in 1978 produced only 19% fewer young than were produced in 1977 (Table 2). In the year of lower total population productivity, each pair that was productive fledged (on the average) 0.4 more young than productive pairs in 1977: however, the average number of fledglings per active nest and the average number of fledglings per nest attempt decreased from 1977 to 1978. This indicates that pairs of Ospreys that failed in 1978 did so early in the nesting cycle either by failing to produce clutches or by losing young nestlings.
Table 5
Frequencies of Clutch- and Resulting Initial Brood-sizes

<table>
<thead>
<tr>
<th>Year</th>
<th>Clutch-size</th>
<th>No. clutches</th>
<th>Total no. broods</th>
<th>Resulting number of broods of each initial size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>1977</td>
<td>2</td>
<td>8</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>22</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>?a</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1978</td>
<td>1b</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>20</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>?a</td>
<td>2</td>
<td>1</td>
<td>—</td>
</tr>
</tbody>
</table>

*a Clutch- and/or initial brood-size unknown but clutch-size not less than one, as determined by adult behavior; at least one nest appeared to have nestlings present as per adult behavior.

b This egg disappeared within 3 days and no other eggs were laid in the nest subsequently.

c Nest could not be reached and no fledglings were observed on or near it.

Productivity patterns.—The analyses of productivity patterns over the 2 years showed that, in general, early initiation of reproduction was advantageous to the successful production of fledglings (combined data from both years). Lower population productivity occurred during the year in which there was a greater range of reproductive effort among pairs (from not breeding to the production of three fledged young) and in which early and late reproductive success was more similarly successful. These data might be explained if the earlier failure of pairs with certain characteristics (e.g., inexperience together, youth, etc.) during more stressful years reduced the competition faced by remaining pairs during the latter portion of the nesting chronology. Changing patterns of foraging success indicated that productive Ospreys were able to provide similar amounts of food in 1977 and in 1978, but that a greater time investment in hunting was required in 1978 (Judge 1981: unpubl.). Characteristics of adults that can influence a pair’s timing of reproduction and subsequent success include age and/or experience of the members of the pair (Coulson 1966, 1977), incubation behavior and/or its coordination between parents (Lack 1968: 148–151, Skutch 1976, Inglis 1977), and the male’s ability to feed the female during egg formation and incubation (during which time female Ospreys in Bahia de los Angeles are dependent upon their mate for food) and his offspring after hatching (see Newton 1979).

A method for comparing patterns of reproductive loss.—The variation between years among several reproductive parameters suggested the need for a method of comparing patterns of reproductive loss between years.
Table 6
Productivity of Ospreys that Initiated Clutches of Three Eggs Early or Late in the Breeding Season

<table>
<thead>
<tr>
<th>Year</th>
<th>Timing</th>
<th>Eggs (%)</th>
<th>Nestlings (%)</th>
<th>Fledgings (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>Early*</td>
<td>33 (55)</td>
<td>27 (64)</td>
<td>19 (73)</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>27 (45)</td>
<td>15 (36)</td>
<td>7 (27)</td>
</tr>
<tr>
<td></td>
<td>Totals</td>
<td>60 (100)</td>
<td>42 (100)</td>
<td>26 (100)</td>
</tr>
<tr>
<td>1978</td>
<td>Early</td>
<td>36 (63)</td>
<td>22 (71)</td>
<td>14 (67)</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>21 (37)</td>
<td>9 (29)</td>
<td>7 (33)</td>
</tr>
<tr>
<td></td>
<td>Totals</td>
<td>57 (100)</td>
<td>31 (100)</td>
<td>21 (100)</td>
</tr>
<tr>
<td>Both years</td>
<td>Early</td>
<td>69 (59)</td>
<td>59 (67)</td>
<td>33 (70)</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>48 (41)</td>
<td>24 (33)</td>
<td>14 (30)</td>
</tr>
<tr>
<td></td>
<td>Totals</td>
<td>117 (100)</td>
<td>73 (100)</td>
<td>47 (100)</td>
</tr>
</tbody>
</table>

* Early and late denote first or second half of laying period.

Table 7
Frequencies of Brood-Sizes and Resulting Number of Fledgings

<table>
<thead>
<tr>
<th>Year</th>
<th>Initial brood-size</th>
<th>No. broods</th>
<th>No. young</th>
<th>Broods (no. young) fledged</th>
<th>Total young fledged (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>1977</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>11</td>
<td>22</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>8</td>
<td>24</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>?c</td>
<td>2</td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>1978</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>9</td>
<td>18</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>7</td>
<td>21</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>?c</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

* Percentage of nestlings from broods of specified size that fledged.

At least one young fledged.

Nestlings were present in nest but initial brood-size unknown.
trolling for possible age and pair-bond effects on clutch-size (Coulson 1966, Klomp 1970:11). This assumed that the relative proportions of age/experience classes remained similar from year-to-year and was not unreasonable in a long-lived species with deferred maturity.

The "fates" of these potential young were calculated from observed breeding failures, egg mortality, nestling mortality, and disappearance of pairs for each year. Observed rates of loss for each year were converted to proportions of the HMP. Loss of potential reproductive success could thus be classified into distinct and non-overlapping categories (Table 8). Although differences in productivity between 1977 and 1978 were not great, use of the HMP emphasized the stage of the breeding chronology wherein differences did occur. The greatest difference in patterns of loss of potential young between years was the increased loss due to inactivity of resident pairs in 1978. This difference was augmented by a small reduction in the number of pairs that were present in the study area in the second year. Proportional loss due to hatching failure was essentially the same during both years and accounted for the greatest loss of potential young Ospreys. Comparisons of the proportions from different populations would allow analyses of the importance and seasonal timing of those factors influencing their reproductive success under different environmental conditions.

**SUMMARY**

The 1977 and 1978 breeding seasons of non-migratory Ospreys (Pandion haliaetus) in the Gulf of California extended from early January through mid-June with a high degree of asynchrony among pairs that was not caused by renesting. Thirty-two and 28 pairs produced eggs in 1977 and 1978, respectively. Mean clutch-sizes (±SE) were 2.7 ± 0.1 in 1977 (N =

---

**Table 8**

**Calculations and Values of the "Hypothetical Maximum Production" (HMP) for the 1977 and 1978 Breeding Seasons**

<table>
<thead>
<tr>
<th>Reduction in potential young due to</th>
<th>1977</th>
<th>1978</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>(%)</td>
</tr>
<tr>
<td>Reduced number of nesting pairs (34 – N) 2.87b</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>Inactive pairs (N – n) 2.87</td>
<td>6</td>
<td>(06)</td>
</tr>
<tr>
<td>Reduced mean clutch-size (2.87 – ᵐ clutches) n</td>
<td>3</td>
<td>(03)</td>
</tr>
<tr>
<td>Hatching failure (no. unhatched eggs)</td>
<td>38</td>
<td>(40)</td>
</tr>
<tr>
<td>Nestling mortality (nestlings – fledglings)</td>
<td>16</td>
<td>(17)</td>
</tr>
<tr>
<td>Fledged young</td>
<td>32</td>
<td>(33)</td>
</tr>
</tbody>
</table>

a No. = number of potential young.

b N = number of pairs occupying nests, n = number of pairs that were active (i.e., laid at least one egg).
28) and $2.9 \pm 0.1$ (N = 24) in 1978. Hatching success (0.6 nestlings per egg) did not differ in the 2 years although the number of young fledged per active nest decreased from 1.0-0.9. Twenty-one pairs in 1977 produced at least one young to fledging ($\bar{x} = 1.5$) and 14 pairs in 1978 averaged 1.9 fledglings. In 1977, pairs that initiated egg-laying during the first half of the laying period were more successful in producing fledglings than were pairs that laid later. Thirty-two fledglings were produced. In 1978, 26 fledglings were produced and there was no significant association of reproductive timing and success.

Success in raising nestlings to fledging was similar in both years, indicating that factors influencing the differential production for the two breeding seasons occurred early in the breeding and/or environmental phenology. A comparison of patterns of reproductive loss indicated that the greatest difference between 1977 and 1978 breeding seasons in patterns of reproduction was an increased loss of reproductive potential due to non-breeding.

ACKNOWLEDGMENTS

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LITERATURE CITED


NESTLING GROWTH AND DEVELOPMENT AND THE BREEDING ECMOLOGY OF THE BEECHEY JAY

SCOTT R. WINTERSTEIN AND RALPH J. RAITT

Studies on the growth and development of young birds provide insight into ecological and social factors such as predation pressure, food supply, and amount and type of parental care that are important to a species during its reproductive cycle (Lack 1968; Ricklefs 1968, 1973, 1979; Case 1978). Studies of cooperatively breeding species are of particular interest because the assistance provided by nonbreeders may affect growth and development patterns (Bateman and Balda 1973, Woolfenden 1978). Many species of New World jays have been found to be highly social, cooperative breeders, but few studies have included a detailed analysis of their growth. Notable exceptions are studies by Bateman and Balda (1973) on Piñon Jays (Gymnorhinus cyanosephalus) and by Woolfenden (1978) on Florida Scrub Jays (Aphelocoma c. coerulescens).

We examined the growth and development of nestlings of the cooperatively breeding, sub-tropical Beechey Jay (Cyanocorax [Cissilopha] beech-eii). We attempt to relate the growth pattern observed to certain ecological and social factors.

The ecology and breeding biology of this large jay of western México were examined by Raitt and Hardy (1979) and Raitt et al. (unpubl.) and are summarized below. Beechey Jays live year-round in groups of two to six individuals on 24–36-ha territories. Each group consists of a nucleus pair of breeders and a varying number of nonbreeding helpers, usually young of previous years that remain on their natal territory and occasionally birds that immigrate from nearby territories. All group members assist in building the nest, feeding and defending nestlings and fledglings, and defending the nest and territory. The breeding season begins with nest construction in mid-May and extends through mid-August, by which time all young are fledged. Groups attempt only one nest at a time and they stop after successful fledging. An unsuccessful first nesting attempt is generally followed by a second attempt. All incubation (18–19 days) and brooding are done by the breeding female. Clutch-size varies from three to five ($\bar{x} = 4.2$) and brood-size from one to five ($\bar{x} = 3.2$). The number of fledglings per group per year averages 2.3.

STUDY AREA AND METHODS

The results discussed herein are part of a 5-year (1974–1978) study on the ecology and breeding biology of Beechey Jays conducted near Mazatlán, Sinaloa, México (Raitt and Hardy
NESTLING almost continuous
Bateman 805 of black
257
9, Eyes of dor sal
low is
and
June,
10 annual averaging irregular of Muscoidea), the primary are to
d multinational, the forest is almost totally barren of green foliage. This dry season is followed by a 2–3 week transition period, with fairly light, irregular rainstorms. The wet season, marked by heavy, almost daily storms, begins in mid-
to late June and continues through late October, with July, August, and September each averaging over 200 mm of rain. Within 3 weeks after the rains begin, the trees and shrubs are fully foliated and a dense herbaceous understory develops.

This study extended from 28 May–30 July 1978. Six nests, belonging to five different groups, were found and each was visited daily until the young fledged (three nests), the nest was destroyed by predators (two nests), or the study ended (one nest). All but one nest had a complete clutch when discovered. The eggs from one nest were weighed to the nearest 0.5 g on the day of discovery, 12–13 days after laying.

Hatching of eggs within a clutch was slightly asynchronous, spanning as much as 24 h per nest. To permit individual recognition, each nestling was marked on the bottom of its toes with a combination of red and blue ink dots. After the nestlings were 1-day old (hatch day = day 0), each nest was visited daily between 16:30 and 19:00. Weight to the nearest 0.5 g and the lengths of all right primaries and rectrices to the nearest 0.5 mm were measured daily for each nestling. As they are exemplary of the feather growth observed, lengths of only primary 9 and rectrix 1 are discussed. Morphological and behavioral changes were noted for each nestling. All observations and measurements were made on the ground a few meters from the nest.

The six nestlings that survived to fledging were used for most of the final analyses of growth and development. Three nestlings, all from the nest that was still being observed at the end of the study and all heavily parasitized with botfly larvae (probably of the superfamily Muscoidea), grew atypically and are considered separately.

GROWTH AND DEVELOPMENT

General development.—At hatching the nestlings were naked, with yellowish red skin through which the viscera were easily observed. The legs were yellow, the bill was dull yellow, and a black egg tooth was present on the upper mandible. By day 5 of the nestling period the dorsal skin surface was dark brown and the ventral skin surface was yellow. By day 10 the egg tooth had disappeared and by day 13 the dorsal skin surface was greenish brown. By fledging at day 22 or 23, the exposed skin of the dorsal surface was red-tinged greenish brown, and the unfeathered portion of the ventral surface was yellow. The bill and legs were also yellow.

The eyes began to open on day 5 or 6 and were fully open one day later. Eyes open at a younger age in Beechey Jays than in Piñon Jays (days 7–9, Bateman and Balda 1973) and within the range reported for Florida Scrub Jays (days 4–7, Woolfenden 1978).

At hatching the nestlings gave soft squeaks and extended their necks
### Table 1

Changes in Weight and Lengths of Primary 9 and Rectrix 1 for Nestling Beechey Jays

<table>
<thead>
<tr>
<th>Age (^a)</th>
<th>Wt. (^b)</th>
<th>P9 (^c)</th>
<th>RI (^d)</th>
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</table>

\(^a\) Age in days since hatching; hatch date = day 0; N = 6 for all days except days 13 and 22, when N = 5.

\(^b\) Mean weight (g) (top number); SD (middle number); range (bottom number).

\(^c\) Mean length (mm) of primary 9 (top number); SD (middle number); range (bottom number).

\(^d\) Mean length (mm) of rectrix 1 (top number); SD (middle number); range (bottom number).
vertically to beg. By day 9 they were able to grasp objects (nest lining, fingers, etc.) with their feet. They were able to stand and move about the nest by day 13. By day 16 they made well-coordinated flapping motions with their wings and hopped around when placed on the ground. By day 18 they were able to perch and just prior to fledging (day 21 or 22) they made short hop-fly journeys into the branches around the nest.

**Feather development.**—At hatching the feather tracts were evident under the skin as areas of small dark dots. All juvenile primary, secondary, and alular feathers had broken through the skin by day 5 (Table 1, Fig. 1). The alar tract of Piñon Jays (Bateman and Balda 1973) and Florida Scrub Jays (Woolfenden 1978) erupted on day 4. Beechey Jays’ capital, humeral, ventral, spinal, and femoral tracts were first evident as blue-gray quills less than 0.5 mm long on day 8. The rectrices erupted on day 9 (Table 1, Fig. 1). Rectrices erupted on day 5 for Piñon Jays and day 9 for Florida Scrub Jays. The crural tract was also first evident on day 9. The first feathers to break through their sheaths were in the alar tract, which did so on day 11 (usually about day 9 for Florida Scrub Jays). Feathers broke through the sheaths by day 13 for all other tracts except the caudal (day 14), humeral (day 15), and capital (day 17). Feathers of the ventral tract were completely free from their sheaths by day 17, femoral and crural feathers by day 18, and humeral and spinal ones by day 19. At fledging the feathers of the capital, alar, and caudal tracts were still partially sheathed. Beechey Jays were well feathered 3–4 days prior to fledging.

**Weight.**—The mean dimensions of 19 eggs measured at the Western Foundation of Vertebrate Zoology, Los Angeles, California, were 32.2 (SD = ±1.1) × 23.0 (SD = ±0.6) mm. The mean weight of 5 eggs, all laid in the same nest and all 12–13 days old was 11.2 g (range = 11.0–12.0 g). Each of these eggs weighed on the average 5.8% of the weight of an adult female (x = 194.0 g, N = 9). While this value is similar to those for fresh egg weights of Florida Scrub Jays (7.6%) and Piñon Jays (6.4%), weight lost by the Beechey Jay eggs during the almost 2-week period between laying and the date weighed may make the result artificially low. The eggs of Black-throated Magpie-Jays (*Calocitta collici*) lost on the average 2.0 g between laying and 14 days of age (Winterstein, unpubl.). Assuming Beechey Jay eggs lost weight similarly (the two species are similar in adult weight and are sympatric), a fresh egg weight of about 13.2 g can be projected. This projected value is 6.8% of the weight of an adult female, within the range for Florida Scrub Jays and Piñon Jays.

Three hatchlings on day 0 had a mean body weight of 8.6 g, 4.4% of adult weight, a value smaller than the 6.0% figure given for Piñon Jays (Bateman and Balda 1973) and Florida Scrub Jays (Woolfenden 1978). This
Fig. 1. Changes in body weight and lengths of primary 9 and rectrix 1 of nestling Beechey Jays. Open symbols indicate nestlings not infected with botfly larvae. For these nestlings $N = 6$ for all days except days 13 and 22, when $N = 5$ and the values plotted are the mean daily values listed in Table 1. Closed symbols indicate nestlings that were infected with botfly larvae. For these nestlings $N = 3$ for all days except day 20, when $N = 2$. Squares are mean daily weights; triangles, mean daily lengths of primary 9; and circles, mean daily lengths of rectrix 1. The line represents the growth curve fitted by the equation given in the text. Hatch date = day 0.
lesser value is not due to a substantially lower hatchling weight (Piñon Jay = 6.3 g, Florida Scrub Jay = 4.8 g), but rather to a much greater adult weight (Beechey Jay = 193.3 g, male and female weights $t = 0.08, N = 18$, NS; Piñon Jay = 103.3 g; Florida Scrub Jay males = 81.7 g and females = 76.7 g).

Weight increased rapidly from hatching until day 13, at which age the rate of increase declined markedly (Table 1, Fig. 1). Additionally, from day 16–19 the mean weights fell below those predicted by the growth curve (Fig. 1). Reduction in the growth rate during the second half of the nestling period may have been related to: (1) a decrease in integument weight as flight feathers became increasingly free of their sheaths and contained less water (Ricklefs 1979); and/or (2) increased allotment of energy for temperature regulation (see Ricklefs 1969, Case 1978).

The procedure used to analyze growth was that of Ricklefs (1967), also used by Bateman and Balda (1973) and Woolfenden (1978). Ricklefs' method requires an accurate determination of the age at fledging for proper interpretation of the results. Five of the Beechey Jay nestlings included in this analysis fledged on day 23 and the sixth on day 22. From 1974–1977, the first 4 years of study of this population of Beechey Jays (Raitt and Hardy 1979, Raitt et al., unpubl.), the average age at fledging was 21.3 days (SD = ±1.5, range = 20–24 days). In this 4-year period, each nestling was handled only one time, for banding. The age of the nestlings at banding ranged from 15–21 days.

The growth curve (Fig. 1) was best described by the logistic equation:

$$W = \frac{A}{1 + e^{-K(t_w-t_0)}}$$

where $W$ is the weight of the bird in grams at day $t_w$, $A$ is the upper weight asymptote in grams approached by the nestling, $e$ is the base of natural logarithms, $K$ is a constant proportional to the specific rate of growth, and $t_0$ is the age in days at the point of inflection on the growth curve (Ricklefs 1967). For Beechey Jays $A$ was 129.9 g (Piñon Jays, 78.9 g; Florida Scrub Jays, 60.0 g). The age at which half of $A$ was attained ($t_0$) was 7.2 days (Piñon Jay, 7.6; Florida Scrub Jay, 8.2). For the Beechey Jay, $K$, the overall growth rate index, was 0.360; slightly higher than that for the Piñon Jay (0.328) and the Florida Scrub Jay (0.335), indicating that although it is a larger bird, the Beechey Jay grows at a faster rate as a nestling.

Another method of comparing growth rates is to determine the time required to grow from 10% to 90% ($t_{10-90}$) of $A$ (Ricklefs 1967, 1968). Based on Ricklefs’ equations for determining observed and expected $t_{10-90}$,
Beechey Jays grew more rapidly than predicted (observed = 12.2 days, expected = 15.2 days), while Piñon Jays grew essentially as predicted (observed = 13.4 days, expected = 13.3 days), and Florida Scrub Jays grew slightly slower than predicted (observed = 13.1 days, expected = 12.3 days).

At fledging, Beechey Jays had attained on the average 67% of adult weight. This is less than for Piñon Jays, 79% (Bateman and Balda 1973), and Florida Scrub Jays, 76% (Woolfenden 1978). In fact, it is less than that listed for 53 of 56 passeres (Ricklefs 1968: Table 2, R value). Value of \( R \) (fledging-to-adult weight ratio) is related to the stage of development of the young at fledging; according to Ricklefs (1968), low \( R \) values are indicative of species in which adults forage on the ground and fledglings escape predators primarily by running. However, adult Beechey Jays seem to forage in trees as often as on the ground and the young remain in the trees after fledging. The unusually low \( R \) value observed for Beechey Jays indicates that much growth occurs after fledging.

**EFFECTS OF BOTFLY PARASITISM**

The brood of three nestlings still in the nest when the study ended were heavily parasitized by botfly larvae. We were unable to fully identify these larvae, but they are probably members of the superfamily Muscoidea. Raitt and Hardy (1976) found that Yucatan Jays (Cyanocorax yucatanica) were similarly parasitized by *Mydaea* sp. (Muscidae). The larvae in Beechey Jays formed subcutaneous cysts in all areas of the body, including the skin around the eyes, the corners of the bill, and the feet and toes. These parasites were first observed when the young were 6 days old. On that day, one nestling (BB) had five larvae, another (BL) had six, and the third (RL) had 11 (Table 2). (Little is known about the life history of the parasite and it was, therefore, unknown exactly how many days elapsed between infection and emergence.) Larvae were first evident on day 6, and healed sores on day 10, suggesting about a 5-day maturation period. Changes in the total number of parasites per nestling (Table 2) indicate that reinfection occurred throughout the nestling period. On the last day on which the nest was visited (day 20), BB had 10 parasites, RL had 14, and BL was dead beneath the nest.

Physiological and morphological events, such as the eruption of particular feather tracts or changes in skin color, occurred at the same age in the heavily parasitized nestlings as they occurred for noninfected nestlings. However, behavioral development appeared retarded. Noninfected nestlings could grasp objects with their feet on day 9; infected nestlings were unable to do so until day 15. Noninfected nestlings could stand and move about the nest on day 13, whereas the infected nestlings could not
Table 2  
Number of Botfly Larvae Infecting Three Beechey Jay Nestlings

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</table>

* No data were available for that day.

** Nestling found dead.

do so until day 19. The infected nestlings made flapping motions on day 19, a behavior first observed on day 16 in the noninfected ones. By day 18 the noninfected nestlings were able to perch and could hop around when placed on the ground. Infected nestlings were never able to perch, nor to hop when placed on the ground. By day 20 (the last day they were observed) the two surviving, parasitized nestlings could no longer support their heads or stand. They suffered from severe spasms that caused their bodies to shake continuously during the measurement period.

Mean daily values for the three growth parameters for infected and noninfected nestlings are plotted in Fig. 1. A modified Friedman rank test, with ranking within days-of-age to remove the effect of growth and a single-degree-of-freedom-contrast (Steel and Torrie 1960), was used to compare infected (N = 3) and noninfected (N = 6) nestlings. Daily weights for the infected nestlings were significantly higher than those for the noninfected ones for the period prior to infection, days 1-5 (Friedman Value, $\chi^2_r = 7.68, P < 0.005$). On the initial day of infection, day 6, the mean weight of the infected nestlings (54.0 g) was almost identical to that of the noninfected ones (53.3 g). From day 7 until day 13 the weights of the infected nestlings did not differ from those of the noninfected ones ($\chi^2_r = 1.73, P$
> 0.10). From day 13 to day 20 the weights of the infected nestlings, a combination of the actual weight of the nestling and the weight of its associated parasites, were significantly greater than those of the noninfected ones ($\chi^2_r = 17.6, P < 0.001$).

The lengths of primary 9 were about the same for both groups (Fig. 1) for days 5–7, but after day 7 those of the noninfected nestlings were significantly greater than those of the infected ones ($\chi^2_r = 36.8, P < 0.001$). The lengths of rectrix 1 of the infected nestlings were significantly shorter than those of the noninfected ones throughout the observation period (Fig. 1; $\chi^2_r = 48.0, P < 0.001$). As the nestling period progressed, presumably a larger portion of the nutrients used in the development of feathers (and other morphological features) was lost to the parasites, causing these significantly reduced lengths.

On day 20, one nestling, BL, was found dead on the ground a few meters from the nest. Although the exact cause of death was not known, we suspect that it died as a result of being parasitized. The only obvious external injuries were the sores from emerged or still developing larvae.

As demonstrated, heavy botfly infestation of three nestlings retarded growth and development and probably caused death. However, when all (1976–1978, including Raitt and Hardy, unpubl. data) infected nestlings, regardless of parasite load ($N = 19$), were compared to all noninfected ones ($N = 21$), no difference existed in the number of nestlings that survived to one year of age ($\chi^2 = 0.15, df = 1, P > 0.50$). The deleterious effects of parasites on survival may have been obscured by the fairly small sample available and the small probability of any fledgling surviving to one year (38%, Raitt et al., unpubl.).

**DISCUSSION**

The growth and development patterns of Beechey Jays are atypical for passerines of their size and for social jays studied thus far. Because of their much larger size Beechey Jays would be expected to grow slower than Piñon Jays and Florida Scrub Jays; however, the opposite is true. At fledging Beechey Jays are only 67% of adult weight, while most passerines are between 80 and 100% (Ricklefs 1968: Table 2) and Piñon Jays and Florida Scrub Jays are both above 75%. Also, the Beechey Jay’s nestling period (22–23 days) should be longer (see Ricklefs 1968, 1979) than that for Piñon Jays (21–22 days; Bateman and Balda 1973), which it equals, and Florida Scrub Jays (17–18 days; Woolfenden 1978), which it slightly exceeds.

The observed growth rate, fledging-to-adult weight ratio, and pattern of development may be adaptations to facilitate breeding in a highly seasonal environment. Complex interactions of food supply and predation pressure,
which are related to the very distinct wet and dry seasons, may have influenced both the time of year when Beechey Jays breed and the duration of their nesting period.

For Beechey Jays, as for most birds (Lack 1968), food supply is probably the ultimate factor most important in influencing the initiation of breeding. Young Beechey Jays generally hatch during the dry season-wet season transition period and fledge soon after the wet season begins (Raitt and Hardy 1979). Moffitt (1980) found that insect numbers on the study site were lowest just prior to the first rains, increased steadily throughout the wet season, and then began to decline steadily when the rains stopped. As insects are the primary food items fed to the young, Beechey Jays cannot profitably initiate breeding any earlier in the year.

Food supply, however, is insufficient to explain why Beechey Jays do not delay breeding until later in the wet season when food is plentiful, or why the young fledge at such an early stage in development. We hypothesize that predation, which accounts for the majority of nesting losses (78%, Raitt et al., unpubl.), is the factor preventing adult Beechey Jays from delaying the onset of breeding and nestlings from remaining longer in the nest. Beechey Jays protect their nest by cooperatively mobbing predators, which they locate primarily by sight. We postulate that after the wet season begins, nests become progressively harder to defend; under the cover of the dense, green foliage, predators presumably can get closer to the nest without being detected. After fledging, the young are fairly mobile and can be hidden quite well in the same foliage that offers cover to predators. Therefore, fledging the young as soon as possible after the wet season begins, reduces losses to predators. Calculated by the Mayfield method (1961, 1975) (and see Winterstein 1980), the probability of producing a fledgling from an egg laid in an early nest (young hatched before the wet season began) was 31%, while that of an egg laid in a late nest (young hatched after the wet season began) was only 17%; the difference was caused entirely by nestlings of late attempts having only one-third the survival probability of those of early attempts. The fact that nests may also become progressively harder for predators to find after the wet season begins may be offset by their ability to remember the location of a nest previously located, but not yet preyed upon.

Predation is not the only risk of remaining in the nest. Because the chances of botfly infection presumably increase as the time in the nest increases and the probability of reinfection certainly does (Table 2), reduction in the length of the nestling period also will reduce losses to parasites.

Shortening the nestling period will not in itself automatically result in an increase in the survival rate of the young; at fledging they must be
mature enough to function out of the nest. The pattern of development must be such that when fledging occurs, functions necessary for survival out of the nest have reached at least some minimal level of development. To survive out of the nest Beechey Jays must have reasonably well-developed locomotor organs and neuromuscular control; in fact they apparently attain that stage of development as early as 2 days prior to fledging. Beechey Jay fledglings are fairly mobile and very inconspicuous shortly after they leave the nest. The fledglings are extremely difficult to locate. Despite extensive searching, only twice in 5 years did we find fledglings that had been out of the nest longer than 1 day, and we were able to follow them for no more than 2 successive days. The rapid development of locomotor organs and neuromuscular control apparently occurs at the expense of overall body weight. This pattern of development will increase the chances of young surviving only if there are no serious disadvantages associated with having a low body weight at fledging. We found that actual weight at fledging had little effect on subsequent survival. Those young that weighed less than the mean weight at fledging for this population were as likely to survive to yearling age as those that weighed more than the mean (\( N = 54, \chi^2 = 1.06, df = 1, P > 0.25 \)) (see also Woolfenden 1978).

The role of mortality factors, including predation and parasitism, in the evolution of growth rates has been the subject of controversy (Ricklefs 1969, 1979; Case 1978). Based on his failure to find a correlation between reported juvenile mortality rates for particular species and the growth rates of these species, Ricklefs (1969:1032) argued that “specific differences in mortality rates are responsible for little, if any, of the observed diversity in growth rates” (but see Case 1978). The relationship we have postulated between predation-parasitism and growth rate in Beechey Jays might be construed as contrary to Ricklefs’ findings. We believe, however, that this is not the case. For example, in a later paper Ricklefs (1976:198) stated that “early fledging must require rapid growth and maturation; both of these factors undoubtedly respond in parallel to variation in nest mortality rate.” We have emphasized the shorter nestling period in Beechey Jays as an adaptation to reduce losses to predators and parasites, and that three adaptations combine to produce the shorter nestling period: rapid growth rate, development that results in relatively precocious locomotor abilities, and fledging at a relatively low body weight.

The above mentioned adaptations may be dependent upon the fact that Beechey Jays are cooperative breeders. The number of helpers at a nest is significantly related to the rate at which the nestlings are fed (Raitt et al., unpubl.), suggesting that the rapid growth rate could be, at least partially, a function of the contributions of helpers (see Case 1978). However, our small sample of nestlings precludes rigorous testing of the relation between feeding rate and growth rate. Also, in the long postfledging de-
velopmental period (full development presumably is not attained until well into or near the end of the wet season), the young are undoubtedly dependent upon the cooperative efforts of all group members for food and protection. The long period of postfledging care presumably mitigates any disadvantages associated with having a low body weight at fledging (see Bateman and Balda 1973, Woolfenden 1978). These latter considerations are necessarily speculative; a definitive analysis of the overall effects of sociality on growth and development requires data on more solitary and cooperative breeders than have been studied to date.

SUMMARY

Nestling growth and development patterns were analyzed for a population of cooperatively breeding Beechey Jays (Cyanocorax [Cissilopha] beecheii) near Mazatlán, Sinaloa, México. Nestlings were found to have a faster growth rate (Ricklefs' K value = 0.360) and shorter nestling period (22–23 days) than would be predicted for jays of their large size. Locomotor organs apparently developed rapidly, at the expense of overall body weight. At fledging the young were only 67% of adult body weight, but very mobile and difficult to locate.

Three nestlings, heavily infected with subcutaneous larval parasites, grew atypically. Physiological and morphological stages were reached at the same age in both infected and noninfected nestlings, but behavioral capabilities in the infected group were retarded. Infected nestlings weighed more than the noninfected ones both prior to being parasitized (day 6) and after day 13 of the nestling period; between days 6 and 13 the weights of the two groups did not differ. Lengths of primary 9 and rectrix 1 of the parasitized nestlings were significantly shorter than those of fledging nonparasitized ones.

The rapid growth rate, low fledgling-to-adult weight ratio, and subsequent short nestling period of normal Beechey Jays are seen as adaptations to facilitate breeding in a highly seasonal environment. Limited food supply during the dry season and intense predation pressure and increased likelihood of being parasitized during the wet season preclude breeding at any time other than the late dry season-early wet season period and strongly select for the shortest nestling period possible. The rapid growth rate of nestlings and survival of fledglings may depend upon the cooperative efforts of all group members.

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LITERATURE CITED


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WATERBIRD MORTALITY FROM BOTULISM TYPE E IN LAKE MICHIGAN: AN UPDATE

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Botulism as a food poisoning is acquired from ingestion of material containing a potent neurotoxin produced by the bacterium *Clostridium botulinum*. Under aerobic conditions, this microorganism exists in a spore stage. In the presence of a suitable nutrient source, favorable temperature, and in the absence of oxygen, vegetative growth can occur. It is in the vegetative stage that botulinal toxin is synthesized within metabolizing cells, and is released upon autolysis of the cell (Rosen 1971). Seven types of botulinal toxins are currently known: types A through G. Botulism outbreaks in humans are usually caused by toxin types A, B, E, and more recently F; outbreaks usually result from improperly prepared or stored food products (Dowell et al. 1970). Suspected cases of botulism type G have recently been reported (Sonnabend et al. 1981). Botulism type D usually occurs in cattle.

Avian mortality from botulism occurs essentially worldwide, most frequently among waterfowl and shorebirds, and is usually associated with type C toxin (Rosen 1971). Annual mortality to botulism type C in North America alone has been in the hundreds of thousands (Rosen 1971). Naturally occurring botulism type E was not reported in birds until 1963 and 1964, when Herman (1964) and Kaufman and Fay (1964) associated type E toxin with extensive die-offs of Common Loons (*Gavia immer*) and gulls (*Larus* spp.) on the Indiana-Michigan shores of Lake Michigan. Mortality was estimated at 7720 in 1963 and 4920 in 1964 (Fay et al. 1965). Another die-off of similar nature in 1965 was reported by Fay (1966); additional mortality attributed to botulism type E in Michigan has since been reported (Monheimer 1968, Graikoski et al. 1970, Stuhl et al. 1977). In the present paper, we report three additional outbreaks of botulism type E in birds in Lake Michigan occurring in 1976, 1980, and 1981, and we present evidence of the natural consumption by loons and Ring-billed Gulls (*Larus delawarensis*) of food items containing type E toxin.

MATERIALS AND METHODS

Carcass examination.—Necropsies were conducted at the National Wildlife Health Laboratory (NWHL) on selected fresh avian carcasses found during epizootics reported herein; carcasses were submitted either chilled (4°C) or frozen. Moribund birds were bled in the field and sacrificed; blood samples were chilled and submitted with the carcasses. Upon
necropsy, lesions were noted and appropriate diagnostic tests were conducted to determine cause of morbidity or mortality. Tests included routine bacterial and viral studies, mouse toxicity tests, and parasite examinations of selected tissues. Tissues from several specimens were analyzed for organochlorine content at the U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center. Mercury levels were determined by the Wisconsin Alumni Research Foundation (now Raltech, Inc.), Madison, Wisconsin.

Demonstration of botulinal toxin.—Serum was separated from blood samples collected from moribund birds and from heart blood of dead birds to test for the presence of type C and type E botulinal toxins. Standard mouse toxicity tests were employed, involving intraperitoneal (IP) injection of 0.5 ml of serum each into unprotected mice (Mus sp.) and into mice protected with type-specific antitoxin. Demonstration of toxin was based on death of unprotected mice and survival of protected mice. Death of unprotected mice and survival of mice protected with type E antitoxin and mice protected with type C antitoxin provided evidence that both C and E toxins were present in the serum sample, though each alone at levels sublethal to mice. This interpretation is based on studies by Jensen and Gritman (1966), who suggest an adjuvant (synergistic) effect between sublethal levels of types C and E toxin when present together in causing mortality in Mallards (Anas platyrhynchos).

Fish samples removed from alimentary tracts of moribund and dead birds were processed by using the extraction method described by Foster et al. (1974). The presence of botulinal toxins was determined by IP injection of 0.5 ml of extract into mice, as described above.

RESULTS

1976 epizootic.—Mortality involving Common Loons along the southeast shore of Lake Michigan was first reported on 22 October 1976 to the Michigan Department of Natural Resources (MDNR). By 4 November, reports were received of dead birds on Michigan beaches from Union Pier to Benton Harbor in Berrien County. On 8 November, an aerial survey conducted by MDNR from the Indiana-Michigan border to Muskegon (about 145 km) disclosed 592 dead loons, 6 moribund loons, and 6 dead gulls (J. Aldrich, pers. comm.). Carcasses were most heavily concentrated along shorelines in Berrien (N = 455) and Van Buren (N = 118) counties; snow cover on beaches north of Van Buren County caused counts in those areas to be incomplete.

Between 26 October and 19 November, 342 avian carcasses (330 Common Loons, 1 Red-throated Loon [G. stellata], 6 unidentified gulls, 1 Oldsquaw [Clangula hyemalis], 2 grebes—an Eared Grebe [Podiceps caspicus] and an unidentified individual, 1 Redhead [Aythya americana], and 1 White-winged Scoter [Melanitta deglandi]) were collected from Lake Michigan shores in Michigan. Searches for additional carcasses were discontinued after 22 November. Total mortality in Michigan was estimated to be between 600 and 1000 birds. An additional 157 dead Common Loons and one gull carcass were also collected along the Indiana shores of Lake Michigan between 2–15 November.

Botulinal type E toxin was demonstrated in blood from carcasses submitted to NWHL and to the MDNR Rose Lake Wildlife Research Center. At NWHL, 21 Common Loons, 1 Ring-billed Gull, 1 Oldsquaw, and 1
Eared Grebe were received for examination. Type E toxin was demonstrated in 8 of 18 loons tested. The gull had a mycotic air saculitis caused by Aspergillus fumigatus. Botulism tests on the Eared Grebe were inconclusive; the Oldsquaw was too autolyzed for examination. Other bacterial and viral studies on these specimens were negative for other etiologic agents.

Analysis of tissues from the Ring-billed Gull and seven loons examined above disclosed organochlorine levels below those considered lethal (Ohlundorf et al. 1978); polychlorinated biphenyl (PCB) residues were slightly elevated (ranging from <0.2–2.5 ppm wet weight in brain tissue, 1.1–14.0 ppm in muscle tissue), but below levels known to have serious effects on birds. Mercury analyses of kidney tissues from two loons also were below levels known to be significant (0.75 and 1.35 ppm). Type E toxin was demonstrated in the remains of an unidentified fish removed from the ventricular of one loon.

1980 epizootic.—A die-off of about 60 Ring-billed Gulls was investigated during 10–25 June 1980 on a small island in southern Green Bay, near Green Bay, Brown Co., Wisconsin. About 1000 gulls were nesting in a colony on this island. Mortalities were composed of about 64% subadult and adult gulls, and 36% gull chicks. In addition, one moribund Black-crowned Night-Heron (Nycticorax nycticorax) was found.

During the die-off, reports were also received of mortality among alewives (Alosa pseudoharengus) and suckers (Catostomidae) along the eastern shores of Green Bay. The cause of that mortality was not investigated. Surveillance of other areas of Green Bay for additional avian mortality was conducted by the Wisconsin Department of Natural Resources. Since no additional dead birds were found, it appeared that mortality was limited to the nesting colony.

Type E botulinal toxin was demonstrated in blood samples from one of five moribund adult gulls, but not in two moribund gull chicks or the Black-crowned Night-Heron. No other pathogens were isolated from the examined birds. The mercury level in the kidney of the Black-crowned Night-Heron was below the lethal level (0.3 ppm), as were PCB (8.6 ppm) and other organochlorine levels in the brain.

Type E toxin was demonstrated in the ventricular contents of two moribund adult gulls. Unfortunately, blood samples from these birds were not tested for presence of the toxin. One dead alewife found on the island was negative for type E toxin.

1981 epizootic.—On 3 November 1981, a report was received by the Illinois Department of Conservation (IDOC) of six dead Common Loons found along a 90-m section of Lake Michigan shoreline near Kenilworth, Cook Co., Illinois. Additional dead Common Loons and Herring Gulls (Larus argentatus) were also reported by the city of Winnetka, Illinois,
and the Metropolitan Sanitary District of Greater Chicago (MSD) on 4–6 November on a 24-km-section of Lake Michigan between Evanston and Lake Forest. A total of 69 dead Common Loons, 8 Herring Gulls, and 17 other birds (reported to be loons and gulls) was collected within this region.

An aerial survey was conducted on 17 November by IDOC to assess the distribution and magnitude of any additional mortality. About 100 km of Lake Michigan shoreline in Illinois were surveyed; in addition, a 1.6-km zig-zag pattern in open water adjacent to the shoreline was surveyed. One unidentified dead bird was observed. Live loons and diving ducks were easily visible from the aircraft.

Six Common Loons and one Herring Gull were examined at NWHL. A pooled sample of heart blood from three additional loons was also received. Types C and E toxin were found in the heart blood of three of the six Common Loons and in the pooled sample from the three additional loons. Only Type E toxin was found in blood samples from one of the six loons and one Herring Gull.

No other pathogens were isolated from carcasses examined at NWHL. PCB levels in three loons were determined independently at the Illinois Department of Agriculture Laboratory in Centralia, and were below those considered lethal (H. Shivaprasad, pers. comm.). Gross and histologic examinations of tissues failed to reveal evidence of infectious or other toxic diseases.

The presence of an oil slick in Lake Michigan off of Evanston during this die-off led to speculation that oiling may have been responsible for the deaths observed. Although one carcass found by the MSD appeared oiled, there was no evidence of petroleum residues on any of the carcasses examined at NWHL.

**DISCUSSION**

The presence of botulinal toxin in the carcass of a bird does not necessarily mean that the bird died from botulism. Postmortem invasion of tissues by *C. botulinum* present in intestinal tracts of birds occurs readily; toxin thus produced under anaerobic postmortem conditions could result in a false positive diagnosis. Additional evidence needed to substantiate a diagnosis of botulism includes demonstration of the toxin in blood samples from moribund birds known to be susceptible, and identification of the source of the toxin.

In the present investigations, type E toxin was demonstrated in blood from 8 of 18 Common Loon carcasses examined in 1976 and five of six loons and a Herring Gull in 1981. In 1980, one of five moribund Ring-billed Gulls had type E toxin in its blood. All three species are susceptible to experimental intoxication by type E toxin (Monheimer 1968). The negative
botulism tests among some dead birds in these studies could have resulted from: (1) insufficient amounts of toxin in samples to produce mortality in unprotected mice; (2) destruction of toxin by proteolytic activity of other postmortem invaders or destructive environmental factors (most carcasses were in poor postmortem condition); or (3) other factors as the cause of death. No other causes of mortality, however, were found in carcasses examined, other than one gull in 1976 which had a mycotic air saculitis. Negative tests in some of the moribund gulls examined in 1980 could be a result of levels of toxin too low to be detected. Fay et al. (1965) likewise found that toxin could seldom be demonstrated in blood from sick birds which remained alive for several days; they suggested this was due to low (undetectable) levels of ingested toxin. Jensen and Gritman (1966), however, found that type E toxin disappeared from the bloodstream of experimentally inoculated Mallards rapidly (by 8 h); thus birds showing clinical signs of botulism may not have detectable levels of circulating toxin.

Type E toxin was demonstrated in fish remains found in the ventriculus of a dead loon and two moribund gulls. It is possible that the toxin in the fish from the loon was formed after the bird had died; however, type E toxin in the fish remains from the moribund gulls confirms the natural ingestion of material containing toxin. Toxin from the fish remains found likely caused the observed morbidity, since clinical signs of botulism can occur in gulls within 3 h of ingestion (Kaufman and Crecelius 1967). This information adds an important link to the epizootiology of botulism type E in the Great Lakes. Although type E toxin has been demonstrated in fish carcasses from the Great Lakes (Monheimer 1968, Graikoski et al. 1970), and the feeding of dead Lake Michigan fish to captive gulls has caused botulism type E mortality (Fay 1966), observations of free-flying gulls and loons consuming material containing preformed toxin and becoming sick have not been previously reported.

With these factors in mind, we believe that mortality in loons and gulls reported herein was due to botulism type E; during the 1981 epizootic, type C toxin was also present and may have enhanced the effects of type E toxin (Jensen and Gritman 1966). To our knowledge, this is the first evidence of concomitant presence of types C and E toxin in naturally occurring mortality. The common documentation of botulism type C mortality in the Great Lakes (Herman 1964; Graikoski et al. 1970; NWHL, unpubl.) leads one to wonder whether the concurrent presence of type E toxin might be obscured during routine testing for type C toxin (Jensen and Gritman 1966). Mortality in species other than loons and gulls found during epizootics cannot be attributed to botulism type E with the present data.

Evidence suggests that botulism type E in gulls and loons is acquired through ingestion of fish containing the toxin. Since fish have been shown
susceptible to type E toxin (Huss and Eskildsen 1974), birds may have consumed intoxicated fish or fish carcasses containing toxin formed after the fish’s death. The widespread presence of *C. botulinum* type E spores in Great Lakes sediments and in a variety of fish species has been well documented (Bott et al. 1964, 1966, 1968; Graikoski et al. 1970; Sugiyama et al. 1970). We would thus expect avian mortality to botulism E to be likewise widespread. The three epizootics reported here give further evidence of its widespread occurrence.

Before 1980, reports of avian mortality to botulism type E were largely limited to autumn occurrences; however, the die-off of Ring-billed Gulls in Green Bay demonstrated that it could also occur in early summer. S. Schmitt (pers. comm.) also reported summer (July) 1981 mortality of 13 loons in Lake Superior in which type E toxin was demonstrated. We do not know whether mortality occurs during other seasons, but it is possible that continual low level losses could occur unnoticed or unreported.

**SUMMARY**

Three outbreaks of botulism type E occurring in waterbirds on Lake Michigan since autumn 1976 are discussed. Natural ingestion of food containing type E toxin by Ring-billed Gulls (*Larus delawarensis*) and the presence of type E toxin in blood from moribund gulls were demonstrated. Concurrent presence of type C and type E botulinal toxins was found in a die-off of Common Loons (*Gavia immer*). In combination with previous reported outbreaks, these incidents suggest that this disease is geographically widespread in Lake Michigan, and that environmental conditions conducive to type E botulinal toxin production and consumption occur in both summer and autumn.

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**LITERATURE CITED**


U.S. FISH AND WILDLIFE SERVICE, NATIONAL WILDLIFE HEALTH LABORATORY, 6006 SCHROEDER ROAD, MADISON, WISCONSIN 53711 (CJB, RMD); ILLINOIS DEPT. CONSERVATION, Lisle, ILLINOIS 60532 (SPG); WISCONSIN DEPT. NATURAL RESOURCES, GREEN BAY, WISCONSIN 54303 (DO); AND U.S. FISH AND WILDLIFE SERVICE, EAST LANSING, MICHIGAN 48823 (LES). ACCEPTED 5 NOV. 1982.
GENERAL NOTES

A comparison of breeding bird census techniques with mist netting results.—
Measuring bird abundance has long challenged ornithologists. Because absolute measures are almost impossible, we rely on several well-known techniques to estimate abundance. Internationally, two basic methods are widely used: the strip transect method and variations of it (Enemar, Vär Fågelvärld 2:1-114, 1959; Emlen, Auk 88:323-342, 1971; 94:455-468, 1977; Järvinen. Ornis Scand. 7:43-48, 1976) and the spot-mapping method (Williams, Ecol. Monogr. 6:317-408, 1936; International Bird Census Committee, Aud. Field Notes 24:722-726, 1970). Transect sampling potentially samples the entire bird community, but it necessarily emphasizes territorial males because of their conspicuousness. Spot-mapping samples only territorial males and thus cannot detect the nonbreeding component of bird populations.

Very few studies have used capture-recapture techniques to estimate song bird abundance (Nichols et al., Studies Avian Biol. 6:121-136, 1981). Borror (Ecol. Monogr. 18:412-430, 1948) used capture-recapture data to estimate the daily numbers of migrant White-throated Sparrows (Zonotrichia albicollis) in Ohio. However, comparisons of traditional bird censusing techniques with capture-recapture data are lacking.

In the present study we compare strip transect sampling, two intensities of spot-mapping for 12 regular species, and data from mist-net captures and recaptures for five bird species. Population estimates of Cardinals (Cardinalis cardinalis) from these techniques are also compared with estimates from extremely intensive mapping of a color-banded population.

Study area and methods.—The study plot was a 4.8-ha (240 × 200 m) pine-hardwood forested area in Nacogdoches County, eastern Texas. Although the area was smaller than normally recommended for spot-mapping (Oelke, Studies Avian Biol. 6:114-118, 1981), the small size permitted intensive netting of bird species and intensive mapping of color-banded Cardinals. Approximately half of the area was mature forest (18-22 m tall) and half a 5-year-old pine plantation with dense pine and deciduous foliage 2-3 m high. The area had patchy foliage and ranged from xeric sandy hill tops to moist sites along two streams. Several small openings with a main ground cover of grasses and forbs occupied about 3% of the area. Dominant tree species in the forested area were shortleaf pine (Pinus echinata), loblolly pine (P. taeda), post oak (Quercus stellata), and sweetgum (Liquidambar styraciflua). Dominant plant species in the pine plantation were loblolly pine, winged sumac (Rhus copallina), smooth sumac (R. glabra), and American beautyberry (Callicarpa americana).

A 40-m grid with numbered stakes and flagged poles positioned at all intersections of grid lines provided reference points for plotting bird locations (Fig. 1). Three strip transects, each 200 m long and 80 m wide, covered the entire study area (see Fig. 1 caption) and were censused as described by Conner and Dickson (Wildl. Soc. Bull. 8:4-10, 1980). While one census taker started transect sampling at one end of the study area, the other census taker started spot-mapping at the other end, thus eliminating time and weather biases. Birds were spot-mapped at distances up to 60 m outside the study plot in order to determine what proportion of partial territories were included in the study plot. Spot-mapping (10.3 total h) always took more time than transect sampling (7.3 total h). Each of the two census takers completed four transect samples and four spot-map samples, totaling eight samples for each technique and cancelling any observer bias resulting from different sampling abilities. The sampling period was 24 May-6 June 1979 between 07:30 and 09:30 CDT. When spot-mapping, observers noted simultaneous singing of conspecific males.

Transect data were recorded in the same manner as spot-map data, noting simultaneous singing of conspecific males on small grid maps of the study area. This permitted using our transect data to double the intensity of our spot-map sampling.
We attempted to obtain an estimate as close as possible to the actual Cardinal breeding population through an intensive effort (234 total h) of spot-mapping, observing, and flushing only color-banded Cardinals from 26 April–6 June 1979. This permitted us to determine nearly exact positions of all Cardinal territorial boundaries. Poor visibility and impenetrability of vegetation did not permit extensive use of Wiens’ (Ornithol. Monogr. 8, 1969) flushing technique.

Eleven mist net (2.1 × 12.8 m with 3.8 cm mesh) distributed throughout the area (Fig. 1) were used to capture birds moving through understory vegetation (0–2 m above the ground). Typically, 5–7 nets were in operation at any one time with netting positions changed weekly. Birds were captured and banded (610 net-h) from 25 April–19 May and recaptured for population estimates from 20 May–14 June 1979. Cardinals were banded with color-bands as well as USFWS metal bands. Sufficient netting data were gathered to calculate a Lincoln index (Davis and Winstead, pp. 235–236 in Wildlife Management Techniques Manual, The Wildl. Soc., 1980) using capture-recapture data on adult Cardinals, Indigo Buntings (Pass-
Table 1
Strip Transect, Spot-map, and Mist Netting Estimates of Bird Abundances in a 4.8-ha Area in East Texas (No. Birds/4.8 ha)

<table>
<thead>
<tr>
<th>Species</th>
<th>Transect sampling (N = 8)</th>
<th>Spot-mapping (N = 8)</th>
<th>Mist netting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Highest no. detected (A)</td>
<td>Highest no. males detected × 2 (B)</td>
<td>No. territorial males × 2 (C)</td>
</tr>
<tr>
<td>Cardinal (Cardinalis cardinalis)</td>
<td>11</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>Indigo Bunting (Passerina cyanea)</td>
<td>8</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Carolina Wren (Thryothorus ludovicianus)</td>
<td>5</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>White-eyed Vireo (Vireo griseus)</td>
<td>5</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>Yellow-breasted Chat (Icteria virens)</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Yellow-billed Cuckoo (Coccyzus americanus)</td>
<td>4</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>Red-eyed Vireo (Vireo olivaceus)</td>
<td>4</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>Black-and-white Warbler (Mniotilta varia)</td>
<td>5</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Parula Warbler (Parula americana)</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Kentucky Warbler (Oporornis formosus)</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Hooded Warbler (Wilsonia citrina)</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Louisiana Waterthrush (Seiurus motacilla)</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>50</td>
<td>70</td>
<td>76</td>
</tr>
</tbody>
</table>

We assumed that species had well-established territories and thus had basically closed populations.

Transect data for each species are evaluated two ways: the highest number of individuals per species detected during any census trip (Method A), and the highest number of males of each species detected per trip (summation technique [Palmgren, Acta Zool. Fenn. 7, 1930]) multiplied by 2, assuming monogamy, to approximate both males and females (Method B, Table 1). Methods A and B tend to overestimate bird abundance per unit area because of the occurrence of partial territories on the edges of the strip transect. Potentially, all males...
with partial or whole territories in the study area could be singing on the study area during a census visit. The relative degree of overestimation should decrease as transect width increases; i.e., as transect width increases, the area of the strip transect increases at a greater rate than does the edge.

Population estimates from spot-mapping are evaluated two ways for each species. Method D is the traditional spot-map estimate based on the sum of whole and fractional territories multiplied by 2 (Table 1). Method D should not be biased toward overestimations of populations even in small study plots if the partial territories located just inside the edge of study plots are accurately measured as a fraction of the whole territory. We measured fractional territories to the nearest one fourth. Method C estimates populations by multiplying the total number of territorial males detected (either whole or partial territories) by 2. Thus, Method C is biased toward overestimates of the number of male birds, especially in small study plots such as ours, because the ratio of partial territories to whole territories tends to increase as study plot size decreases.

Results and discussion.—Comparisons of transect and spot-map data revealed that total birds estimated with spot-mapping (Method C) was somewhat higher than both transect estimates (A and B, Table 1). Standard spot-mapping (Method D), which is not biased toward overestimating birds, yielded a higher estimate of total bird abundance than transect Method A. Total birds estimated with transect Method A was 88% of the total estimated with Method D.

Our transect estimate (Method B) using number of males × 2 was 92% of the estimated total number of territorial male birds (including partial territories) that inhabited the study area × 2 (Method C). This comparison (B with C) is valid because both methods estimate whole and partial territories. Other comparisons of transect sampling with spot-mapping have been less favorable toward the efficiency of transect sampling (Franzreb, Condor 78: 260–262. 1976; Dickson, Am. Birds 32:10–13, 1978).

Increasing the intensity of spot-mapping (16 vs 8 samples) did not substantially increase estimates of bird abundance. The number of territories was increased by one-half for two species: Cardinals and Yellow-breasted Chats. This supports Robbins’ (pp. 142–163 in Proc. Workshop Management, Southern Forests for Nongame Birds, U.S.D.A. For. Serv. GTR SE-14, 1978) recommendation of 8–10 census trips per plot where available time for the observers is a factor.

A Lincoln index (mark/recapture ratio) population estimate was calculated for five species (Table 1). The high estimate of 60 resident Yellow-breasted Chats is undoubtedly incorrect and probably caused by a high incidence of active migrants in the study area. Low site tenacity of residents may have also contributed to the high turnover (Thompson and Nolan, Ecol. Monogr. 43:145–171, 1973).

Lincoln index estimates for the Cardinal (7 of 10 marked birds were recaptured), Indigo Bunting (7 of 20 recaptured), Carolina Wren (three of six recaptured), and White-eyed Vireo (four of five recaptured) populations were also higher than any of the transect or spot-map estimates (Table 1). Lincoln estimates for Indigo Buntings were somewhat higher than the other three species when compared to transect and mapping estimates. Some movement of resident buntings in and out of the area may have contributed to an inflation in this population estimate. Netting results indicated a sex ratio close to 1:1 for Cardinals, Carolina Wrens, and White-eyed Vireos. However, we netted twice as many female Indigo Buntings as males. It is likely that our netting “recapture” period sampled late female migrants for buntings, thus slightly inflating our Lincoln index population estimate and yielding a 2:1 female to male sex ratio (C. S. Robbins, pers. comm.). A less likely alternative is that Indigo Buntings on the study area were polygynous.

Lincoln index estimates for Cardinal, Carolina Wren, and White-eyed Vireo populations
in the study area may be more accurate than the estimates for chats and buntings. Our supporting data for this speculation, for Cardinals at least, are the results from 234 h of intensive spot-mapping in the study area for color-banded Cardinals. This intensive Cardinal mapping revealed a total of 10 territorial males (20 Cardinals total) to have all or part of their territory in the study area, three more males than spot-mapping (Method C) detected (Table 1). Twenty Cardinals (10 territorial males × 2) is the same population number estimated by the Lincoln index (Table 1). It is important to note that Method C and the Lincoln index estimates both sample males with whole or partial territories in the study area, thus comparisons between these two methods are fairly valid.

We also treated our 234-h Cardinal mapping data as standard spot-map data, summing whole and fractional territories, in order to compare them with standard eight-sample spot-mapping (Method D). A total of seven whole Cardinal territories were detected using the intensive (234 h) Cardinal spot-mapping, two more whole territories than detected via eight sample spot-mapping. Thus, standard spot-mapping (D) estimated about 71% of what may have been close to the actual Cardinal breeding population. Svensson (Acta Ornith. 14:322–338, 1974) and Best (Auk 92:452–460, 1975) have suggested that considerable variation can exist between persons delineating territory boundaries from spot-maps. Thus, some of the difference in Cardinal population estimates in our study may be from interpretational errors.

Our field observations also suggested that there may have been more Cardinals on the study area than even the 234 h of intensive mapping or netting demonstrated. In addition to the 10 territories that were well delineated, several “floater” males often tried to wedge new territories at junctures of three established Cardinal territories. These males, and possibly some females, were apparently not included in the Lincoln estimate from netting data. These “floating” males were usually driven off or delayed in setting up a territory until one of the established pair’s nest failed or their young successfully fledged.

We also found the nest of a color-banded male (red-left) that fledged young, but sang very rarely. Territories of other males that sang regularly seemed to encompass part of the area red-left frequented. We were unable to delineate red-left’s territory even with 234 h of intensive mapping.

Our observations suggest that all the techniques we evaluated underestimate bird populations. Spot-mapping Method C and transect Method B both yielded estimates that were highest and closest to estimates from our netting results. Yet, even the overestimating biases of these two methods were apparently more than compensated for by bird inconspicuousness. The netting results and intensive spot-mapping of Cardinals suggest that both transect sampling and spot-mapping census techniques underestimate bird populations because they are incomplete samples.

Acknowledgments.—We thank L. B. Best, J. T. Emlen, A. Enemar, O. Järvinen, C. S. Robbins, T. Root, and R. C. Szaro for constructive comments on the manuscript. This project is endorsed and funded in part by the U.S. Man and the Biosphere Program (MAB–3) contributing to grazing land management objectives. We thank the John Cason family and the Southland Division of St. Regis Paper Co. for use of their lands during the study.—RICHARD N. CONNER, JAMES G. DICKSON, AND J. HOWARD WILLIAMSON, Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with The School of Forestry, Stephen F. Austin State Univ.), Southern Forest Experiment Station, U.S.D.A. Forest Service, Nacogdoches, Texas 75962. Accepted 10 Oct. 1982.
Incomplete songs and associated behavior of Sage Sparrows.—The Sage Sparrow (Amphispiza belli) is a locally-common breeding bird of sagebrush (Artemisia tridentata) in the intermountain west. Vocalizations of this species have only recently been described in detail (Rich, Condor 83:113–119, 1981; Wiens, Auk 99:208–229, 1982). The intent of this note is to provide additional information on Sage Sparrow vocalizations, especially in regard to incomplete songs.

In 1976 and 1977 I studied the behavior of four unmarked, neighboring, territorial males from March to July in Bingham County, Idaho. Males are identified by numbers; male 3 was present in both years and is referred to as male 3–6 for 1976 data and male 3–7 for 1977. For details see Rich (1981). Each male had one song type that did not vary appreciably throughout most of the breeding season or, apparently, from year-to-year.

Males also had calls that Miller (U.S. Natl. Mus. Bull. 237, Pt. 2, 1004–1013, 1968) referred to as tsip and “harsh” notes. The tsip note was a high, thin call note typical of sparrows. The “harsh” note was a rapidly repeated note of rasping quality, each with a rising inflection. These calls were usually used separately, but on a few occasions I heard the tsip notes intensify to “harsh” notes in a graded manner. Females did not sing and may or may not use the “harsh” notes. Females did use tsip notes.

The only significant exception to the stereotyped song of the male was the incomplete song wherein only a few syllables to about half the full song were sung. The incomplete song always began with the first syllables of the complete song and had the quality of being abruptly truncated. There were well-defined behavioral relationships in the four males that used it (Table 1). The common factor was the close association with the female. However, there was also an influence from the stage of the breeding cycle as all four males were observed with the female at other times during the breeding season but did not sing incomplete songs when with her at that period. Incomplete songs were never heard after spring arrival and prior to nest-building, during incubation, during the nestling period, or after the fledging and dispersal of the last brood when complete songs were sung. Two other males, 1–7 and 17, gave both tsip and “harsh” notes while with the female prior to nest-building and in territorial conflicts where contact and visual displays (unilateral wing raise, head bobbing) occurred. The tsip and “harsh” notes were associated with agonistic situations and were secondarily associated with incomplete songs which seemed to occur in sexual contexts.

Incomplete songs, when sung, either comprised the entire song bout or were distributed among the complete songs of the bout. In the four males the distribution of complete and incomplete songs in 60 bouts with both types was random (one-sample runs test, all $P > 0.05$, Zar, Biostatistical Analysis, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974). But in males 3–6, 3–7, and 6 incomplete songs occurred more frequently early in the bouts; 60% of first songs were incomplete, 43% of second songs, 31% of third songs, and an average of 18% of the songs at later positions. Perhaps motivation was highest at the onset of a bout and dropped off during the bout. The percentage of incomplete songs in all bouts in which they occurred was similar for the four males: male 3–6, 22%; male 6, 22%; male 3–7, 20%; male 4, 40%. The higher percentage was given by male 4 mainly on one day when he sang incomplete songs while he accompanied the female and young of the first brood around the territory.

The Eurasian Blackbird (Turdus merula) sings only part of its song when inviting the female to leave the nest and forage (Stork, Z. Tierpsychol. 28:54–58, 1971). Brémond (Behaviour 58: 99–116, 1976) experimenting with truncated songs of Bonelli’s Warbler (Phylloscopus bonelli) noted that they were less effective in arousing aggressiveness in males than were full-length
sung. In some warblers (*Dendroica* spp.) (Morse, Nature 226:659–661, 1970; Anim. Behav. 24:764–771, 1976), the Grasshopper Sparrow (*Ammodramus savannarum*) (Smith, Wilson Bull. 71:141–152, 1959), Clay-colored Sparrow (*Spizella pallida*) (Knapton, pers. comm.), Cuban Grassquit (*Tiaris canora*) (Baptista, J. Orn. 119:91–101, 1978) and White-eyed Vireo (*Vireo griseus*) (Bradley, Auk 98:80–87, 1981) there are two songs, one of which is used primarily in epigamic situations and the other in territorial or agonistic contexts. The Sage Sparrow, not having a varied vocal repertoire, may use the incomplete song under certain conditions of high motivation as an alternative to his one stereotyped song. Perhaps communication of aggressive tendencies to the female is reduced. Alternatively, incomplete songs may simply result from a conflict between approach and avoidance (Ficken and Ficken, Behaviour 46:114–128, 1973; Wunderle, Anim. Behav. 27:982–996, 1979; J. B. Falls, pers. comm.). In this respect I have also observed Brewer’s Sparrows (*S. brevirostris*) begin truncating songs when another male flew to a nearby perch and also in response to playback of full song. Several vireos (*Vireo* spp.) also sing truncated but faster songs in response to playback (Barlow, pers. comm.). Thus, conditions of increased stimulation, coupled with uncertainty, may obstruct full-length songs in the Sage Sparrow.

It would be interesting to document the presence or absence of incomplete songs in other species that are known to have a single stereotyped song. If incomplete songs are not used perhaps other variations of full song occur to enhance communication of different motivational states.

**Acknowledgments.**—Observations were made while conducting research supported by The Frank M. Chapman Memorial Fund of the American Museum of Natural History and by a Grant-in-Aid from Sigma Xi. I thank L. F. Baptista, J. B. Falls, and C.H. Trost for comments on an earlier version of this note.—TERRILL RICH, Dept. Biology, Idaho State Univ., Pocatello, Idaho 83209. (Present address: P.O. Box 642, Shoshone, Idaho 83252.) Accepted 7 July 1982.

### Table 1
**Behavioral Relationships of Incomplete Songs of Sage Sparrows**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Male 3-6</th>
<th>Male 3-7</th>
<th>Male 4</th>
<th>Male 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Near female during nest-building</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Chasing female</td>
<td>X</td>
<td>X</td>
<td>0°</td>
<td>0</td>
</tr>
<tr>
<td>After young fledged from first nest</td>
<td>X</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>With fledged young and female</td>
<td>—2</td>
<td>—</td>
<td>X</td>
<td>—</td>
</tr>
<tr>
<td>Immediately after desertion of nest</td>
<td>X</td>
<td>—</td>
<td>—</td>
<td>X°</td>
</tr>
<tr>
<td>With <em>tsip</em> notes</td>
<td>X</td>
<td>X</td>
<td>0</td>
<td>X</td>
</tr>
<tr>
<td>With &quot;harsh&quot; notes</td>
<td>X</td>
<td>X</td>
<td>0</td>
<td>X</td>
</tr>
</tbody>
</table>

1. Incomplete songs occurred (X).
2. Condition not observed (—).
3. Condition observed but incomplete songs not sung (0).
5. Deseretion of first nest, cause unknown.
Incubation period of Ring-billed Gulls and the egg immersion technique.—Incubation period has been reviewed generally (Drent, pp. 332–340 in Avian Biology, Vol. 5 [Farner and King, eds.], Academic Press, New York, New York, 1975), and treated specifically for larids (Parsons, Ibis 114:536–541, 1972; Nisbet, Nature 241:141–142, 1973; Courtney, Ibis 121:207–211, 1979). Intra-clutch differences in incubation period have not been discussed for the Ring-billed Gull (Larus delawarensis), although the incubation period for the third egg has been reported (Vermeer, Can. Wildl. Serv. Rept. Ser. No. 12, 1970).

Stage of incubation in some birds can be determined by immersing an egg in a beaker of water and measuring the degree of rotation or flotation of the egg. Eggs that have not yet been incubated lie horizontally on the bottom of the beaker. During the course of incubation an egg, upon immersion, will first rotate (i.e., its blunt end gradually rises), then float and break the surface of the water. The degree of rotation or flotation is an index of the egg's specific gravity, which can be used to estimate the laying and/or hatching date of the egg (Westerskov, J. Wildl. Manage. 14:56–67, 1950; Schreiber, Condor 72:133–140, 1970; Hays and LeCroy, Wilson Bull. 83:425–429, 1971). The immersion technique has apparently not been applied to eggs of Ring-billed Gulls. Our objective was to determine the incubation period for each of the three eggs in the clutch of the Ring-billed Gull and to determine the usefulness of the immersion technique as a predictor of laying and/or hatching dates.

We conducted our study in April and May 1980 at the Eastern Headland, Toronto Outer Harbour, Lake Ontario, Toronto, Ontario (for description of the study area see Blokpoel and Fetterolf, Bird-Banding 49:59–65, 1978). To determine the sequence of laying and the laying interval, we staked 60 nests, each containing one egg, and checked all nests daily between 10:00 and 12:00 until each contained a complete clutch of three eggs. Eggs were marked A, B, and C to identify first, second, and last egg, respectively, using a felt marker. Chicks were subsequently referred to as A-, B-, and C-chicks, respectively.

We gently released each egg in a beaker of fresh water and measured the degree of egg rotation at the bottom of the beaker using a transparent protractor. Once the eggs floated, we used calipers to measure the diameter of the portion of the egg above the water surface. Once the clutches were complete, each nest was visited every other day. When hatching began, most nests were visited daily. All nests studied were of birds nesting during the first nesting peak in mid-April. All breeding birds in our sample were in full adult plumage (i.e., no brown or black flecking on body, wing, or tail feathers).

As the A- and B-eggs of ring-bills show some development before clutch completion (Ryder and Somppi, Wilson Bull. 89:243–252, 1977), and as the adults are known to begin sitting on the eggs immediately after laying the A-egg (P. M. Fetterolf, pers. comm.), we define the incubation period of an egg as the period between laying and hatching of that egg. Eggs could be as much as 24 h old when we first located them.

We measured length and breadth of all eggs to the nearest 0.1 mm to calculate egg volume, using the formula: volume = 0.489 × length × breadth² (Ryder, Wilson Bull. 87:334–542, 1975). Statistical analysis included 2-way analysis of variance, Duncan’s multiple-range test, and linear regression.

Incubation period.—Hatching intervals were short compared to laying intervals. The median laying interval between A- and C-eggs was 4 days (N = 58). The median hatching interval between A- and C-eggs was 1 day (N = 46). Incubation periods (±SD) for eggs with respect to their position in the clutch were: A-egg, 28.1 ± 1.3 days (N = 54); B-egg, 26.3 ± 1.1 days (N = 52) and C-egg, 24.8 ± 0.9 days (N = 51).

We tested for intra-clutch differences in volume of eggs. The C-egg was significantly (P <
Fig. 1. Rotation and flotation measures of A-, B-, and C-eggs of Ring-billed Gulls during 22 days of incubation after clutch completion. Vertical lines indicate 95% confidence intervals. Sample sizes are shown above the vertical lines.
0.01) smaller than the A- and B-eggs (Duncan’s multiple range test). Mean volumes (±SD) were as follows: A-egg, 50.4 (±3.7) cm³; B-egg, 50.0 (±3.8) cm³; and C-egg, 47.2 (±3.7) cm³.

To test whether there was a correlation between incubation period and egg volume, we calculated correlation coefficients between these two variables using volumes of A-, B-, and C-eggs separately, as well as the pooled values of the A-, B-, and C-eggs. In the latter case an average incubation period was used as the dependent variable. The resulting relationships in all four correlations were positive but weak (r < 0.10 in each case).

In early-nesting Ring-billed Gulls incubation begins after laying the A-egg, but occurs only during the daytime (Fetterolf, Can. J. Zool. 57:1190-1195, 1979). During the night, until about day 8, the birds desert the colony resulting in cooling of the eggs. Despite that nocturnal desertion, the A-embryo, as judged from egg immersion measurements, has developed to some extent by the time the C-egg is laid.

How then does the C-embryo effectively catch up in its development resulting in a high degree of hatching synchrony within the clutch? The A-egg is significantly larger (as measured by volume) than the C-egg. Smaller eggs develop faster with the same application of heat (Skoglund et al., Poultry Sci. 27:709-712, 1948) which suggests that the C-egg may catch up solely because of its smaller size. The lack of strong correlation between egg size and incubation period in our sample might be explained by assuming that (1) larger eggs were laid by larger females and (2) larger females apply more heat to their eggs. Parsons (Ibis 114:536-541, 1972) found that an increase of 20% (11 cm³) in the volume of Herring Gull (L. argentatus) A-eggs resulted in an increase of about 16 h in the incubation period. In Ring-billed Gulls the difference in volume between the A- and C-eggs is only 6% (3 cm³) but the resulting increase in incubation period is about 36 h. The difference between the two species may be caused by differences in the amount of time spent incubating during the laying period and in the effectiveness of incubation during that period.

If the C-egg in Ring-billed Gulls is smaller partly to facilitate synchronous hatching of the clutch, then the disadvantages resulting from a smaller C-chick at hatching apparently do not outweigh the advantages accrued by hatching synchrony. A slightly smaller C-chick, hatched shortly after the A- and B-chick, may be an adaptation to fluctuations in availability of food during the chick-rearing period (Parsons 1972). If food is abundant the C-chick could easily be raised to fledging; if food is scarce, the C-chick would soon die after hatching because of a disadvantage in competing for food with its older, larger siblings. In situations of intermediate food abundance, being small might be advantageous to the C-chick in that it could survive on a relatively small amount of food.

The egg immersion technique.—Some of the eggs, upon immersion, began to break the water’s surface by day 7, whereas others did not do so until day 17. The A-egg showed signs of hatching (starred or pipped) on day 19, and the C-egg on day 27. With respect to laying sequence of the eggs, confidence limits of flotation measures were widest for the A-eggs and narrowest for the C-eggs, particularly from day 1 to day 9 (Fig. 1). In all eggs, variability was greatest during the period of complete submersion and smallest during the period when the egg broke the water surface. On average, the A-eggs rotated and floated higher than the C-eggs, while the B-eggs were intermediate (Fig. 1).

The egg immersion technique gave highly variable results for eggs incubated for equal lengths of time after clutch completion. Thus, the method is not adequate for determining the stage of incubation, unless the age categories are divided into groups as large as 1 week.

Schreiber (Condor 72:133-140, 1970), using the egg immersion technique for eggs of Western Gulls (L. occidentalis) reported little variation in rotation and flotation in eggs of the same age and suggested that it “would be valuable to compare egg flotation characteristics of other species in order to develop a workable flotation scale for various incubation periods.”
Schreiber checked only two clutches from laying to hatching (floating the eggs five times), but he also floated 100 other eggs whose hatching dates were known (27 of these eggs were floated four times). Schreiber presented no data on incubation periods for individual eggs (A, B, and C), but he reported that incubation periods for completed clutches varied from 25–29 days. Because Schreiber’s methods differed from ours and because it is not clear what incubation period he used for the 100 eggs of known hatching date, his results and our findings cannot be properly compared.

Hays and LeCroy (Wilson Bull. 83:425–429, 1971), using the egg immersion technique for Common Terns (Sternula hirundo), concluded that the stage of incubation of eggs can be estimated within approximately 2 days. The difference in their findings and ours with respect to the usefulness of the technique is probably due to: (1) small, non-representative variability in flotation measures as a result of their small sample size (N = 2 for each of nine categories of embryo development), (2) their use of C-eggs only, resulting in lower variability than that when all three eggs are used, and (3) possible inter-species differences.

Variability among adults with respect to time spent incubating and efficiency of heat transfer from the body to the eggs may result in differences in the rate of development of the embryo, and hence in differences in the rate of change in specific gravity. These then result in differences in rotation and flotation measures at similar stages of incubation.

We thank the Toronto Harbour Commissioners for allowing us to work at the Eastern Headland. P. M. Fetterolf and G. D. Tessier helped in the field. P. M. Fetterolf provided unpublished information. G. E. J. Smith provided statistical advice. J. E. Bryant, S. G. Curtis, R. W. Schreiber, and an anonymous referee commented on earlier versions of the manuscript. Financial support to the senior author was provided by contracts from the Canadian Wildlife Service.—ERICA NOL, Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1, Canada; and HANS BLOKPOEL, Canadian Wildlife Service, 1725 Woodward Dr., Ottawa, Ontario K1A 0E7, Canada. Accepted 29 Oct. 1982.


Communal harvesting of a transient food resource in the Mexican Jay.—Increased efficiency in locating and harvesting transient food resources has been implied as a possible advantage to members of communal groups (Brown. Ann. Rev. Ecol. Syst. 9:123–135, 1978), but descriptions of such events do not seem to have been recorded for communal species. The following incident was observed in the Chiricahua Mts., Arizona, 6 June 1979. At 09:45 a banded female Mexican Jay (Aphelocoma ultramarina), MOOMXO, which had been singing quietly 3 m from me, flew to a patch of sunny, bare ground and began picking up and swallowing winged reproductive ants as they emerged from their nest, paused in the sun, and flew away. She took 18 ants in about as many seconds, and flew to a tree. A few seconds later BOXR, a 1-year-old bird, flew to the spot and took 50 reproductives before I had to look away, again at about one per second. Within 2 min a total of nine jays, most of the flock of 13, arrived and rapidly consumed the ants. By 09:55 the emergence was over, and no reproductives remained at the site. In about 10 min a transient food source had been discovered and shared among nine birds.

It is not clear how the recruits learned of the presence of the food, but Mexican Jays typically watch each other when foraging and are quick to go to the site of a discovery by another jay. Soft calls are continually given by members of a foraging group, and these might have been involved. More conspicuous as signals of food, however, are the swift, direct glides to the spot. Although it is possible that all nine birds would have found this resource
without signals from other birds, the speed with which the birds assembled suggests otherwise. Even a slight delay would have meant loss of some of the food from the group.

Although it is generally acknowledged that birds in flocks profit energetically from each others’ discoveries of food, the possibility of advantage to the discoverer, beyond the food it consumes, does not seem to have been considered. In this case MOOMXO probably profitted in other ways too. As the oldest member of the unit (at least 11 years old) and as a member since the study began in 1970, she was probably related to others in the unit (Brown and Brown, Science 211:959-960, 1981). In addition, some of the recruits fed some of the winged ants to the nearby fledglings, which included those of MOOMXO together with those of two other females. MOOMXO may also have been related to these other fledglings. Thus, there is a distinct possibility that MOOMXO benefitted her indirect fitness as well as her direct fitness (Brown and Brown, Symp. Natural Selection and Social Behavior, Chiron Press, New York, New York, 1981) by calling the attention of her flock members to this transient resource.

I have observed similar, though less dramatic and less thoroughly documented, instances of rapid exploitation of emergences of reproductive ants in the Mexican Jay and the Grey-crowned Babbler (Pomatostomus temporalis).

I thank Mr. and Mrs. E. Bagwell, and Dr. and Mrs. M. Cazier for their gracious permission to make observations on their properties and the Southwestern Research Station of the American Museum of Natural History for permission to use their facilities. This research was sponsored by a research grant (MH16345) from the U.S. Public Health Service.—JEHRELM. BROWN, Dept. Biological Sciences, State Univ. New York, Albany, New York 12222. Accepted 31 Aug. 1982.


Effect of unlimited food availability on the breeding biology of wild Eurasian Tree Sparrows in West Malaysia.—Ward and Poh (Ibis 110:359-363, 1968) suggested that Eurasian Tree Sparrows (Passer montanus) in Singapore initiate and finish breeding and molt 2–3 months earlier than conspecifics in South China, thereby completing these energy-consuming activities before food becomes scarce for Singapore birds. They observed that tree sparrows in Singapore (1°N) breed mainly from January to mid-May. The molt of primaries barely overlaps the breeding season and terminates by late August when the testes of adult males have fully regressed. The marked decline in the number of sparrows sighted and in mean adult body weight which occurred from October to December indicate a period of low food abundance.

If the timing of breeding and molt in tree sparrows is responsive to local food availability, then a population with year-round access to high-quality food should either breed continuously, as does the Common Moorhen (Gallinula chloropus) (Siegfried and Frost, Ibis 117:102-109, 1975), or at least extend its breeding season if the necessity for gonad rehabilitation precludes continuous breeding (Lofts and Murton, pp. 1–107 in Avian Biology, Vol. 3, Farner and King, eds., Academic Press, New York, New York, 1973). I studied the effect of unlimited food availability on the timing of breeding and molt of tree sparrows at the Universiti Pertanian Malaysia (UPM) campus (Serdang, Selangor: W. Malaysia: 3°N) where these birds congregated at the Poultry Unit to feed freely on the enriched commercial mash (17% protein and 3.2% calcium by dry weight) provided to laying hens. The “natural” tree sparrow diet consists of grass seeds and insects which are only seasonally abundant (Nawawi and Jantan, Science and Education Diploma Program Third Year Project Report, Universiti Pertanian Malaysia.
1977). A study of marked individuals mist-netted at the Poultry Unit confirmed that these sparrows were residents, nesting in inaccessible sites of the masonry of nearby buildings and returning regularly to feed on the mash (Hamdan et al., Science and Education Diploma Third Year Project Report, Universiti Pertanian Malaysia, 1977).

Study area and methods.—The UPM campus is within the West Coast Rainfall Region of Peninsular Malaysia which experiences high rainfall during the intermonsoon periods in April and October–November, and low rainfall during February and July (Dale, Trop. Geog. 13: 23–37, 1959) (see Table 1).

From July 1976–June 1977, four mist nets were used to collect tree sparrows in one morning (08:00–10:00) of each month at the Poultry Unit. Nets were placed close to chicken sheds to minimize the visibility of the mesh to sparrows coming in to feed; very few birds were caught as they left the Unit after feeding since the nets were conspicuous against the sky. Sparrows were weighed soon after capture to the nearest 0.5 g and then were sexed by dissection. The length of the usually larger left testis in each adult male was measured to the nearest mm. The broadest dimension of the ovary in adult females was similarly measured whereas the diameter of the largest follicle was measured to the nearest 0.5 mm; oviduct condition, well-developed or not, was also noted. After post-juvenal molt subadults were distinguished from adults by the degree of cranial ossification. The occurrence of molt (feather growing in sheath) was also recorded.

Results.—There was significant [males: F(11, 81) = 10.04, P < 0.001; females: F(11, 71) = 10.07, P < 0.001] and similar monthly variation in mean gonad size of both males and females (Fig. 1a,b). Birds of both sexes measured in July 1976 and in the period December 1976–June 1977 had significantly larger gonads than birds measured in the period August–November 1977 (Scheffé test, P < 0.001). The pattern of variation in maximum follicle size (Table 1) parallels the pattern of gonadal development described above, with enlarged follicles observed in months when ovaries were enlarged (Pearson product-moment correlation, r = 0.61, P < 0.01). Females with muscular, well-developed oviducts were collected from February–June 1977.

Adult males and females did not show the same pattern of weight change (Fig. 2a,b). Males collected in the period September–December 1977 were significantly heavier than males collected in other months (Scheffé test, P < 0.001) but the mean body weight of adult females did not vary seasonally (F(11, 74) = 1.34, P > 0.10).

Although body molt was observed in all months except May 1977, a higher proportion of molting adults was collected during August–November 1976 (Table 1). Similarly, higher proportions of adults molted primaries from August–October 1976 but, unlike the pattern observed for body molt, this was followed by a period of 3 months (November 1976–January 1977) during which primary molt was not observed. In subsequent months there was no discernible trend in the frequency of primary molt observed in the population samples; but in 2 months, March and June 1977, primary molt did not occur. Sparrows in various stages of post-juvenal molt were present in all months except January 1977 and comprised 50% or more of the samples collected in August 1976, and May and June 1977 (Table 1).

Discussion.—These data strongly suggest that the breeding season of tree sparrows on the UPM campus may be at least 2 months longer than that of tree sparrows in Singapore. Three lines of evidence support this. Firstly, enlarged gonads occurred in males and females from December 1976–June 1977 and this presumably marked the time during which breeding was physiologically possible. Secondly, newly fledged juveniles appeared in early February 1977. If the time between oviposition and fledging of a brood for Malaysian tree sparrows is about the same as in temperate populations (30–35 days; Bethune, Gerfaut 51:387–398, 1961; Chia et al., Acta Zoologica Sinica 15:527–536, 1963; Pinowski, Ekol. Pol. 16:1–58, 1968; Seel, Ibis 110:129–144, 1968), then egg-laying began as early as late December on the UPM cam-
Fig. 1. Monthly variation in gonad size of adult Eurasian Tree Sparrows on UPM campus (±SE, N given): (a) length of left testis; (b) broadest dimension of ovary.

pus. Food supplements experimentally presented to Great Tits (Parus major) (Källander, Ibis 116:365–367, 1974), to Carrion Crows (Corvus corone) (Yom-Tov, J. Anim. Ecol. 43:479–498, 1974), and to Kestrels (Falco tinnunculus) (Dijkstra et al., Ibis 124:210–213, 1982) have been shown to significantly advance the laying date of the first egg. Finally, well-developed oviducts were observed in females sampled during the period February–June 1977.

Fig. 2. Monthly variation in body weight of adult Eurasian Tree Sparrows on UPM campus (± SE, N given): (a) adult males; (b) adult females.

that oviposition has occurred in the recent past (oviduct involution requires 10–15 days in White-crowned Sparrows [Zonotrichia leucophrys] [Lewin, Condor 77:46–59, 1975], and about 8 days in several species of African finches [R. B. Payne, pers. comm.]) or that oviposition will occur in the near future. Conservatively estimated, the breeding season of the UPM sparrows ends in mid-June if the observed, well-developed oviducts are regarded as undergoing involution. If the reproductive condition of the UPM sparrows in July 1976 is typical, however, then the breeding season of this population can be reckoned as ending in August and, thus, lasting 8 months.

House Sparrows (Passer domesticus) commence molt of the juvenal plumage from 4–6
**Table 1**

**Monthly Rainfall, Maximum Follicle Size, and Proportion of Juveniles and Molting Adults in Monthly Samples of Eurasian Tree Sparrows on UPM Campus**

<table>
<thead>
<tr>
<th></th>
<th>Jul '76</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan '77</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>June</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall (mm)</td>
<td>58</td>
<td>214</td>
<td>170</td>
<td>371</td>
<td>287</td>
<td>247</td>
<td>283</td>
<td>111</td>
<td>106</td>
<td>175</td>
<td>104</td>
<td>195</td>
</tr>
<tr>
<td>Maximum follicle size (mm)</td>
<td>8.0</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>4.0</td>
<td>4.0</td>
<td>11.0</td>
<td>8.0</td>
<td>12.0</td>
<td>2.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Total no. birds</td>
<td>9</td>
<td>16</td>
<td>9</td>
<td>17</td>
<td>13</td>
<td>32</td>
<td>13</td>
<td>39</td>
<td>39</td>
<td>23</td>
<td>28</td>
<td>25</td>
</tr>
<tr>
<td>Juveniles as % total</td>
<td>22</td>
<td>50</td>
<td>33</td>
<td>18</td>
<td>15</td>
<td>21</td>
<td>0</td>
<td>18</td>
<td>26</td>
<td>35</td>
<td>57</td>
<td>64</td>
</tr>
<tr>
<td>No. of adults</td>
<td>7</td>
<td>8</td>
<td>6</td>
<td>14</td>
<td>11</td>
<td>25</td>
<td>13</td>
<td>32</td>
<td>29</td>
<td>15</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>Percent adults in body-molt</td>
<td>14</td>
<td>50</td>
<td>33</td>
<td>29</td>
<td>27</td>
<td>8</td>
<td>8</td>
<td>6</td>
<td>3</td>
<td>7</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Percent adults molting primaries</td>
<td>14</td>
<td>25</td>
<td>33</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>27</td>
<td>17</td>
<td>0</td>
</tr>
</tbody>
</table>
weeks after leaving the nest (Summer-Smith. The House Sparrow, Collins, London, England, 1963). Should tree sparrows follow a comparable schedule, then the presence of juveniles exhibiting the early stages of post-juvenile molt in all monthly samples except January 1977 suggests that the breeding season at UPM may exceed 8 months. Admittedly, the evidence presented above for an extended breeding season is circumstantial and need to be corroborated by more direct breeding data from a longer term study on the UPM campus. The arguments presented would also be strengthened if a nearby sparrow population depending only on naturally occurring foods can be shown to have a breeding schedule similar to the Singapore population.

Geographic variation does not account for the suggested difference in the breeding schedules of the UPM and Singapore sparrow populations since tree sparrows breed earlier and for a longer period of time with decreasing latitude (Table 2). The UPM population, located 2° north of Singapore, appears to have a breeding season that is 2–3 months longer than the Singapore population, a pattern which is contrary to the above geographic trend. This marked difference also contrasts with the gradual rate of latitudinal variation shown in Table 2; the Singapore population differs from sub-tropical populations (23°N) with respect to duration of the breeding season by about 1 month and from temperate populations (50–52°N) by about 2 months. Climatic differences between the UPM and Singapore sites are negligible (Dale 1955, Nieuwolt, pp. 27–39 in Animal Life and Nature in Singapore, Chung, ed., Singapore Univ. Press, Singapore, 1973) in comparison with these more northern sites.

The observed molting pattern supports my interpretation that increased food availability is the principal factor which prolongs the breeding season of the UPM sparrows. Breeding and molting are energy-consuming activities and most bird species in the S. E. Asian tropics postpone molt until breeding has been completed (Ward and Poh 1968; Fogden, Ibis 114: 308–343, 1972; Wong, unpubl.). The tree sparrows which fed at the UPM Poultry Unit, however, molted body feathers year-round (except May 1977) and molted primaries during most of the breeding season (Table 1). The absence of primary molt in the March and June 1977 samples suggests that for the birds collected in these months, breeding activity may have been energetically too demanding for molt to occur simultaneously. However, two females nearing oviposition (egg with albumen layer in oviduct) in April 1977 were actively molting primaries. This ability to breed and molt simultaneously when high-quality food is continually available has also been reported for the Common Moorhen (Siegfried and Frost 1975).

The pattern of weight change in the UPM tree sparrows also indicates that food availability was continuously high. The post-breeding weight loss observed in the Singapore population was attributed to a decrease in food abundance (Ward and Poh 1968). In contrast, adult male sparrows on the UPM campus showed a significant post-breeding weight gain which persisted until the following breeding season, suggesting that food was readily available and that body weight was only depressed by the energetic demands of breeding. Since both parents in this species share in breeding activities from nest-building to feeding nestlings (Chia et al. 1963), it is surprising that females did not show a fluctuation in body weight similar to that of the males. Females may undertake a greater share of post-fledging care, and consequently do not manage to gain weight after the breeding season. However, observations of individually marked sparrows would be necessary to determine whether this suggested difference in parental behavior might account for the difference in the pattern of weight change observed, since this species is not sexually dimorphic in plumage.

It would be of interest to determine why the UPM tree sparrow population does not in fact breed continuously. Changes in photoperiod and temperature can probably be discounted as factors which serve as cues in scheduling reproductive activities since neither vary appreciably throughout the year (Ward, J. Zool., Lond. 157:25–45, 1969). I was unable to determine whether breeding adults and nestlings use the poultry mash to the same degree
<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude (°N)</th>
<th>Breeding season</th>
<th>Duration (months) of breeding</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Warsaw, Poland</td>
<td>52</td>
<td>mid-Apr.–early Aug.</td>
<td>3</td>
<td>Pinowski (1968)</td>
</tr>
<tr>
<td>Oxford, England</td>
<td>52</td>
<td>late Apr.–late July</td>
<td>3</td>
<td>Seel (1968)</td>
</tr>
<tr>
<td>Marke, Belgium</td>
<td>51</td>
<td>late Apr.–early Aug.</td>
<td>3</td>
<td>Bethune (1961)</td>
</tr>
<tr>
<td>Kwantung, China</td>
<td>23</td>
<td>end of Mar.–Aug.</td>
<td>4</td>
<td>Caldwell and Caldwell, South China Birds,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hester May Vanderburgh, Shanghai, China, 1931</td>
</tr>
<tr>
<td>Hong Kong</td>
<td>22</td>
<td>March–August</td>
<td>4</td>
<td>Webster and Phillips, A New Guide to the</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Birds of Hong Kong, Sino-American Publishing Co., Hong Kong, 1976</td>
</tr>
<tr>
<td>Serdang, Malaysia</td>
<td>3</td>
<td>Dec.–June or July</td>
<td>7–8</td>
<td>Present study</td>
</tr>
<tr>
<td>Singapore</td>
<td>1</td>
<td>Jan.–mid-May</td>
<td>5</td>
<td>Ward and Poh (1968)</td>
</tr>
</tbody>
</table>
since nests were inaccessible. However, the stomachs of adult sparrows collected at the Poultry Unit were found to contain 80–97% poultry mash by weight (Nawawi and Jantan 1977). Chia et al. (1963) observed that insects constitute 91% of foods consumed by tree sparrow nestlings. Although the poultry mash's nutritive value may be comparable to or even surpass that of insects, its granular texture may prevent successful transport to the nestlings. If nestlings must be fed insects, then the discontinuity in breeding may occur when the abundance of insects suitable for feeding young is low. The molt and rainfall data presented in Table 1 suggest that the termination of reproductive activities may in part be controlled by the need to complete molt before the period of heavy rains. The curtailment of breeding and molt in the UPM tree sparrow population, in spite of the continuous and unlimited availability of high-quality food, indicates that the occurrence of these activities can be extended under favorable food conditions only up to a point. The ultimate extent of breeding may alternately be limited by the availability of suitable food to feed the young, and by the necessity to molt, which appears to be regulated by an endogenous schedule (Snow, Ibis 118:366–401, 1976) to avoid the period of heavy rains.

Acknowledgments.—S. Gopal, S. Mat, and Z. A. Manaf aided in the collection of sparrows. M. Mustaphar, Mokhtaruddin and A. Tahar of the Soil Science Department at UPM kindly provided the rainfall data they compiled. This paper was improved by comments from P. F. Becker, S. M. Goodman, Lord Medway (now the Earl of Cranbrook), D. A. Nelson, R. B. Payne, R. W. Storer, and D. W. Wells. Peace Corps Malaysia and the Faculty of Science and Environmental Studies of the Universiti Pertanian Malaysia provided living expenses and logistical support, respectively, during the study. Computer funds for statistical analyses and fellowship support were provided by the University of Michigan's Division of Biological Sciences during the paper's preparation.—MARINA WONG, Dept. Biology, Universiti Pertanian Malaysia, Serdang, Selangor, West Malaysia. (Present address: Bird Division, Museum of Zoology, Univ. Michigan, Ann Arbor, Michigan 48109.) Accepted 30 July 1982.


Foraging dives by post-breeding Northern Pintails.—Dabbling ducks (Anatini), including Northern Pintails (Anas acuta), typically feed by “tipping-up” (Bellrose, Ducks, Geese, and Swans of North America, Stackpole Books, Harrisburg, Pennsylvania, 1976) in shallow water. Pintails are not as adapted for diving as members of the Aythyini or Oxyurini (Catlett and Johnston, Comp. Biochem. Physiol. 47A:925–931, 1974); however, incidents of foraging dives by small numbers of pintails have been reported (Chapman et al., Br. Birds 52:60, 1959; Bourget and Chapdelaine, Wildfowl 26:55–57, 1975). This paper reports on forage diving by a flock of several hundred pintails. Ecological explanations are suggested to account for the behavior and comparisons with tip-up feeding are presented.

Materials and methods.—Feeding pintails were observed with the use of a spotting scope (40X) between 11:00 and 14:00 on a 100-ha pond on Sacramento National Wildlife Refuge, Glenn Co., California, 22 September 1980. Data were collected in two ways with a stopwatch. Method 1: Dive and tip-up durations (period of head immersion) and “pauses” between dives and tip-ups of 133 individual (may include some repeat observations of the same birds) pintails were timed. Method 2: 20 other individuals were observed continuously for variable periods up to 2.5 min. The number of dives or tip-ups seen during the observation period was recorded for each bird.

Water depth was measured at dive and tip-up feeding locations. Five benthic samples (Swanson, J. Wildl. Manage. 42:426–428, 1978) were taken randomly within a 2-m-diameter
circle each at a location where pintails were diving for food and another location where birds were feeding by tipping-up. Each sample included about 800 ml of water at the diving sites and 400 ml at the shallow tip-up sites. Seeds and invertebrates were isolated from the samples, enumerated, dried, and weighed.

The number of pintails present on the study pond was visually estimated. Proportions of feeding birds diving and tipping-up were estimated by scanning through the flock three times using the spotting scope. The feeding behavior of each bird encountered along the sight line in the middle of the field of view was recorded. Collection of data by age and sex was not feasible because differentiation among definitive basic plumages of adults and juveniles and basic I plumages of immatures (Palmer, Handbook of North American Birds, Vol. 2 Waterfowl. Pt. 1. Yale Univ. Press, New Haven, Connecticut, 1976) was not reliable at the approximately 600-m distance from which observations were made.

Results.—Tip-up feeding behavior was first observed on 10 September 1980, shortly after initiation of pond flooding. Diving was first noticed on 20 September and had ceased by 25 September.

About 4000 pintails were present on the study pond. An estimated 1500 of these were actively feeding during the data collection period. Approximately half of the feeding birds were diving and half were tipping-up. Diving birds were located in central portions of the pond in water 60–150 cm deep, whereas pintails tipping-up were scattered around the edges in water 18–24 cm deep.

Pintails seemed to follow the same pattern for a typical dive as described for Mallards (A. platyrhynchos) (Mylne, Br. Birds 47:395, 1954). In addition, diving pintails often traveled several meters forward under water during dives and along the surface between dives. Tipsing birds moved little during and between tip-ups.

Food available to pintails at both diving and tip-up locations was virtually the same. Swamp timothy (Helechloa schoenoides) (Mason, A Flora of the Marshes of California, Univ. California Press, Berkeley, California, 1957) seeds made up nearly 95% by dry weight of the food items in benthic samples at both locations. Other seeds present at both sites included bulrush (Scirpus acutus), smartweeds (Polygonum spp.), and dock (Rumex fueginus). One dipteran pupa and one adult beetle were present in samples at the diving location.

Mean number and dry weight of timothy seeds in the benthic samples at diving locations (923 ± 215 seeds, 0.174 ± 0.45 g) did not differ significantly (Student’s t = 0.712, 8 df, P > 0.05 for number; Student’s t = 0.735, 8 df, P > 0.05 for weight) from those at tip-up locations (709 ± 209 seeds, 0.131 ± 0.038 g). Timothy seeds were the same size at both sites (about 0.185 × 10⁻³ g/seed).

Mean duration of dives (6.48 ± 0.20 sec) and tip-ups (6.50 ± 0.48 sec) was the same (Student’s t = 0.037, 81 df, P > 0.05). Pause duration, however, was almost twice as long for diving birds (5.16 ± 0.36 sec) as for birds tipping-up (2.65 ± 0.49 sec) (Student’s t = 3.944, 48 df, P < 0.001). Thus, the total mean time of a dive sequence (sum of dive and pause duration) was about 2.5 sec longer than the mean time of a tip-up sequence (tip-up plus pause duration). The number of dives per minute (4.93 ± 0.13) was significantly less (Student’s t = 6.304, 18 df, P < 0.001) than the number of tip-ups per minute (7.04 ± 0.31) because of the longer pauses in the dive sequence.

Discussion.—Forage diving by pintails on a large scale as reported here is likely a rare event. However, it seems to be repeated under similar food and water conditions, as I again observed the phenomenon during September 1981. Large flocks of pintails using a foraging method thought to be unusual suggests that food being sought was highly preferred, and/or very abundant. Analysis of esophageal contents of pintails collected while tip-up feeding along the edge of the study pond indicated that swamp timothy was virtually the only food taken during September (Miller, unpubl.). Diving pintails were far from shore (300–400 m)
and could not be collected because of the absence of approach cover. But, based on the high degree of similarity of benthic-water column samples from diving and tip-up areas, extensive examination of the pond bottom before flooding, and known food selection of pintails in the area, I concluded that diving birds were also feeding on swamp timothy. Newly flooded swamp timothy marsh is always heavily used for feeding by pintails in the Sacramento (Miller, unpubl.) and San Joaquin valleys (Connelly and Chesmore, California Fish and Game 66: 233–237, 1980; Beam, unpubl.; Eulis, unpubl.).

Previous reports of forage dives by dabbling ducks suggest that the birds were forced to dive because shallow feeding areas were frozen over (Bourget and Chapdelaine 1975), food was in short supply in shallows (Cottam, Condor 47:39, 1945) or because birds were responding to availability of high energy grains such as wheat (Triticum aestivum) and corn (Zea mays) (Kutz, J. Wildl. Manage. 4:19–20, 1940, Cottam 1945; Chapman et al. 1959). Pintails observed during this study were not forced to feed on swamp timothy by diving. Timothy was available in the same pond and neighboring habitat in densities readily acquired by tipping-up. Also, other foods such as rice (Oryza sativa), millet (Echinochloa crusgalli), and smartweeds were available nearby and being used by large numbers of pintails.

Diving for food in deep water must be energetically more costly for pintails than tipping-up for the same food in shallow water. Animals would not likely use a higher energy consuming method of foraging unless it conferred some advantages, perhaps increased search efficiency (Norberg, J. Anim. Ecol. 46:511–529, 1977). Pintails may have obtained enough additional food to offset the high energy costs of diving, in which case diving behavior would have been related to efficient consumption of a highly preferred food. However, benthic sample size was not sufficient to reliably measure possible food quantity differences between the two feeding sites. Conclusions based on optimal foraging theory are not warranted without additional research.

Although this was a fortuitous observation, management implications are evident. Pintails are highly adaptable in their ability to obtain food under less than ideal conditions. However, swamp timothy could be made more accessible by managing water levels to allow tip-up feeding. Swamp timothy is obviously a preferred food, and habitat management could be used to improve stands at favorable sites.

Acknowledgments.—I thank B. Aldrich, D. Gilmer, R. MacLandress, K. Miller, and D. Raveling for helpful suggestions and critical review of the manuscript. C. LeFever processed benthic samples. I thank J. Beam and N. Eulis for access to unpublished food habits data.—Michael R. Miller, U.S. Fish and Wildlife Service, Wildlife Research Field Station, 6924 Tremont Rd., Dixon, California 95620. Accepted 9 July 1982.

Wilson Bull., 95(2), 1983, pp. 296–297


The incident reported here occurred at 10:00 on 21 October 1979 on the southwest corner of Tule Lake National Wildlife Refuge, Siskiyou Co., California. It was a clear day with no
Observations at the wind. An adult California Gull (Larus californicus) was flying east 5 m above the water, 50 m from the shore, close to 150 Barn Swallows (Hirundo rustica) that were foraging low over the water. One swallow, heading west, passed 1 m below the gull, which dropped suddenly and caught the swallow with its bill, glided for a few meters and settled on the water. The gull proceeded to manipulate the swallow in its bill for 30 sec before swallowing the still moving bird head first. The gull sat on the water for 20 min, then continued its flight to the east.

Most reports of adult birds being taken by gulls have occurred while the prey were on land or water, e.g., Manx Shearwater (Puffinus puffinus) and Common Puffins (Fratercula arctica) in nesting colonies as they go to and from their burrows (Harris 1965), sick or injured birds up to the size of geese (Witherby 1948), Rock Doves (Columbia livia) (Jyrkkänen 1975) and Eurasian Starlings (Sturnus vulgaris) (Drost 1958) at grain piles and ground-dwelling birds which associate with gulls (e.g., Witherby 1948). Gull predation of adult birds on water is much rarer but does occur (Hafft, Condor 73:253, 1971).

Attacks and capture of avian prey on the wing has rarely been reported and generally occurs over sea on migration (Drost 1958). Bannerman (1962) reports Herring Gulls (L. argentatus) capturing and eating Redwings (Turdus musicus) and Eurasian Blackbirds (T. merula) as they migrate over water by knocking the weary birds into the water.

The present account of gull predation on a Barn Swallow, while not a new method of capturing prey as evidenced by gulls catching flying insects, it is the first report of avian prey being captured in this manner.—Stephen A. Laymon, Dept. Forestry and Resource Management, Univ. California at Berkeley, Berkeley, California 94720. Accepted 15 Oct. 1982.


Factors affecting feeding and brooding of Brown Thrasher nestlings.—The nesting period is a particularly stressful time in the lives of birds. In altricial species, the time and energy demands upon parent birds are great and are related to the requirements of their offspring and to environmental factors affecting the adults. Recently, many studies have examined nesting growth and energetics (e.g., Ricklefs, Ibis 115:177–201, 1973; Ricklefs, Publ. Nuttall Ornithol. Club 15:152–292, 1974; O’Connor, Symp. Zool. Soc. Lond. 35:277–306, 1975; O’Connor, J. Zool. Lond. 185:147–172, 1978). Most studies of parental behavior are of cavity-nesting species, probably because of the relative ease of collecting observational data at nest boxes (e.g., Kluiver, Ardea 38:99–135, 1950; Kessel, Am. Midl. Nat. 58:257–331, 1957; Pinkowski, Wilson Bull. 90:84–98, 1978; Walsh, Wilson Bull. 90:248–260, 1978). In contrast, fewer researchers have quantified factors affecting parental care in open-nesting passerines. In our study, patterns of feeding and nest attendance during the nesting period were observed in male and female Brown Thrashers (Toxostoma rufum) in relation to nesting age, time of day, and weather.

Study area and methods.—The study was conducted near Ames, Story Co., Iowa during May–July 1978 on a 15-ha pasture used for grazing cattle. The vegetation was a mixture of woodland and shrub habitat (67%), interspersed with grassland (26%). A stream (7%) meandered through the hilly, lightly grazed range.

Feeding frequencies and nest attendance (time spent brooding and shading) were recorded at four nests with brood sizes of two, three, four, and five young, respectively. Before hatch a portable blind was set up about 20 m from the nest, and a small mirror (10-cm diameter) was positioned above the nest to facilitate watching its contents with 20 × 60 binoculars. Observations began as soon after hatch as possible and continued throughout the nesting
period. Each brood was watched daily in alternate 3-h shifts: dawn to 09:00, 09:00–12:00, 12:00–15:00, 15:00–18:00, and 18:00 to dusk. Thus, all daylight hours were sampled every 2 days; broods were observed an average of 68 h each. One adult at each nest was captured during the incubation period by using a mist net and marked with colored leg bands and a spot of paint on the head. Sex was determined by examining the incubation patch: females had no feathers in the patch, whereas males had a few. Females also had thicker, more vascularized skin in the patch than did males. Individual nestlings were identified by painting the top of the bill with colored enamel (Best, Wilson Bull. 89:625–627, 1977a). Ages of nestlings were divided into 24-h intervals beginning at the time of hatch (0–24 h = 0 day old, 25–48 h = 1 day old, etc.).

Brooding and shading behaviors were distinguished because they evidently serve opposite functions. Brooding occurred when the adult settled down on the nestlings and presumably provided them with heat. During shading, the adult perched on the nest rim with wings slightly spread over the young, protecting them from direct sunlight and possible overheating. (Occasionally adults shaded when no sunlight struck the nest directly.) The percentage of the nest bowl naturally exposed to direct sunlight during 30-min periods was estimated as 0, 1–25, 26–50, or 51–75%. Temperature was monitored hourly. Rainfall was categorized on the basis of its intensity and duration during 30-min intervals: none, light rain <50% of the time, heavy <50%, light ≥50% and heavy <50%, heavy ≥50% and light <50%, and heavy 100%.

Results and discussion.—Both male and female adult Brown Thrashers incubate the eggs (males about 29% and females 71% of the time) (Erwin, J. Tenn. Acad. Sci. 10:179–204, 1935; Partin, Breeding Biology and Behavior of the Brown Thrasher (Toxostoma rufum), Ph.D. diss., Ohio State Univ., Columbus, Ohio, 1977) and care for their young. The relative contribution by each sex in feeding the nestlings varied among broods. In three of the four pairs observed, males fed the young significantly more frequently than females over the nestling period (63% vs 37%, respectively; \( \chi^2 = 101.8, \text{df} = 1, \text{N} = 1404 \) feeding trips, \( P < 0.01 \)). At the fourth nest, the male fed significantly less than the female (44% vs 56%, respectively; \( \chi^2 = 6.6, \text{df} = 1, \text{N} = 397, \ P < 0.05 \)). According to previous studies, female Brown Thrashers generally feed the young more often than males (Gabrielson, Wilson Bull. 24:65–94, 1912; Erwin 1935; Partin 1977). Three males also aided females in brooding the young. The male that did not brood was also the male that fed less than his mate, indicating some variability among individual thrashers and pairs in these behaviors.

Brooding, shading, and feeding of nestlings were related to nestling age, time of day, and certain weather factors. The sample size was inadequate to test for brood-size effects, although they have been documented in other species (e.g., Royama, Ibis 108:313–347, 1966; Mertens, Ibis 111:11–16, 1969; Walsh 1978; Johnson and Best, Auk 99:148–156, 1982).

During the first 2 days after hatch, the adults spent a relatively large percentage of their time brooding the young, but nest attendance had declined to a low and constant level once the nestlings were 5 days old (Fig. 1; see also Partin 1977). Frequency of feedings by both parents increased with nestling age up to 6 days, then leveled off. The increased energy requirement and reduced need for protection against inclement weather as nestlings grew older resulted in an inverse relationship between feeding frequency and nest attendance, but the relationship was significant only for female parents (females: \( r [\text{Pearson product-moment}] = -0.26, \text{N} = 581, P < 0.01 \); males: \( r = -0.08, P < 0.10 \)). Several passerines exhibit a similar pattern of adult feeding and attendance behavior during nestling development (for reviews, see Kendeigh, Ill. Biol. Monogr. 22, 1952; Skutch, Parent Birds and Their Young, Univ. Texas Press, Austin, Texas, 1976).

Brooding comprised most of the time spent in nest attendance (Fig. 1). The pattern of change in brooding time with nestling age was the same for all three males that brooded.
That males spent noticeably less time brooding than females on the day of hatching (0 day old) could be an extension of the difference between the sexes with respect to incubation behavior; the eggs hatch asynchronously, thus, while the first hatchlings are being brooded, the yet unhatched eggs are being incubated. The decline in time spent brooding by males after day 1 paralleled that of females and probably was linked with the development of endothermy in the nestlings (Dunn, Condor 77:288–293, 1975). Males ceased to brood by the time the young were 6 days old, and daytime brooding by females occurred only during rain and/or in the early morning and late evening when temperatures fell below 20°C. Nestlings were brooded at least part of the night until fledging (the females were almost always on the nest at dusk and at dawn).

All four males shaded their nestlings until they were about 6 days old, although time spent shading by males was negligible (less than 5% of the total time) compared with that of females. Shading behavior was apparently related to the amount of sunlight on the nest and to ambient temperature rather than to nestling age (see discussion on weather effects).

Only the first 6 days of the nestling period were included in the analysis of nest attendance relative to time of day. After that, only the female brooded and shaded the young; these behaviors accounted for very little of her time.

Females brooded most in early morning (06:00–07:00) when ambient temperature was lowest (Fig. 2). Then brooding rate by females dropped to its lowest level for the day, even though temperatures were still relatively cool. All four females showed this pattern. After fasting all night and spending a relatively large amount of time in the first few daylight hours brooding and feeding the young, females may require a relatively long feeding bout to replenish their depleted energy reserves. Brooding by males seemed unrelated to time of day or weather patterns associated with time of day.

Shading behavior peaked abruptly between 12:00 and 15:00, when ambient temperature and light intensity reached their daily highs (see also Best, Auk 94:308–319, 1977b; Fischer.
Several investigators have related diurnal changes in nest attendance to ambient temperature rather than to time of day as such (e.g., Fautin, Wilson Bull. 53:107–122, 1941; Cox, Wilson Bull. 72:5–28, 1960; Weeden, Auk 83:368–388, 1966; Skutch 1976). In several species, in which only females brood, time spent brooding declines steadily as temperature increases, reaches a low point in the afternoon, then sometimes rises in the evening (e.g., Kendeigh 1952:74; Cox 1960; Nolan, Ornithol. Monogr. 26, 1978; Johnson and Best 1982). When data from the entire nestling period were included in the analysis, Brown Thrashers also seemed to loosely follow this pattern. During the last half of the nestling period brooding by females was confined almost entirely to early morning and early evening.

Time of day evidently had little effect on how frequently nestlings were fed by either adult (Fig. 2), even though brooding and shading by both adults fluctuated widely so that they did not have the same amount of time available each hour for feeding trips. In contrast, other authors have found that overall feeding rates vary with time of day (Kluyver 1950, Kessel 1957, Cox 1960, Best 1977b, Pinkowski 1978). These diurnal changes have been related to the amount of time the female spends brooding and to the increased begging intensity of young immediately before and after their overnight fast.

Rainfall also influenced behavior of both adults. Mean time spent brooding by females increased steadily as rainfall intensity and duration increased; however, sample sizes for the individual rainfall classes were small. Females brooded an average of 4 of 30 min with no
Fig. 3. Feeding trips by male and female Brown Thrashers and average time spent brooding and shading by both adults in relation to ambient temperature. (Hourly periods with rain were excluded from this analysis.)

rain and increased brooding to 28 of 30 min during continuous heavy rain. Brooding by males during a rainstorm was rare; if the male was at the nest when rain began, he usually brooded the young but almost always was relieved immediately by the female (see also Partin 1977).

Female feeding frequencies decreased as rainfall increased. When rain lasted less than 50% of the time during the 30-min intervals, feeding trips per 30 min averaged 1.6, but when rain occurred more than 50% of the time, only 0.3 feeding trip per 30 min was made. No feeding occurred during continuous heavy rain. Male feeding rates varied widely among the rainfall classes, possibly because of small sample sizes. Rainfall has a strong depressing effect on feeding rates in other species (Kluyver 1950; Gibb, Ibis 92:507-539, 1955; Johnson and Best 1982).

Parental behavior also was related to ambient temperature (Fig. 3). Time spent brooding by males and females decreased as temperature increased from 10-30°C (females: Y [linear regression] = 35.49 - 1.12X, F[1,224] = 42.05, P < 0.001, r² [coefficient of determination] = 0.16; males: Y = 7.99 - 0.23X, F = 7.38, P < 0.01, r² = 0.03). An inverse relationship between brooding time and ambient temperature also has been reported by others (Best 1977b, Johnson and Best 1982).
Shading young occupied only a small portion of the adults’ time when temperatures were below 30°C but increased sharply in occurrence at higher temperatures. The relationship between time spent shading by females and ambient temperature is exponential in Gray Catbirds (*Dumetella carolinensis*) (Johnson and Best 1982).

Adults began shading when the temperature reached 20°C and sun shone on the nest (shading occurred only rarely when sunlight was not on the nest; see Table 1). This suggests that overheating of the young is not likely at temperatures below 20°C, even if sunlight is striking the nest; thus, the adults did not shade. Lower ambient temperatures, however, usually occur in the early morning and evening when light intensity also is lower (r [ambient temperature vs light intensity] = 0.37, N = 237, P < 0.01).

The number of feeding trips per h for males and females was relatively constant over the range of temperatures sampled, with males feeding consistently more than females (Fig. 3). Males spent considerably less time in nest attendance than females, so they potentially had more time for feeding.

Although adults spent relatively little time shading the young, it was important when the sun shone directly on the nest (Table 1). In three nests (broods of three, four, and five young), time spent shading by females increased logarithmically with the amount of sunlight striking the nest (log female shading time [per 30 min] = 0.014 + 0.017·[% of nest in sunlight], F(1,2) = 35.44, P < 0.05, r² = 0.99). (In the analyses above, the mean shading time per 30 min [average for all three broods] for each of the four nest exposure classes [see methods] was regressed against the mid-points of the exposure classes.) Females spent much more time shading than males at all levels of nest exposure to sunlight; there was not enough data on shading by males to test statistically.

Nestlings usually moved away from direct sunlight and occupied a shaded part of the nest whenever possible. When the young could not escape the sun, they depended upon shading by the adults. Female Gray Catbirds increased time spent shading until sun shone directly on about 50% of the nest (Johnson and Best 1982); at higher exposures, shading time leveled off. When compared with female Brown Thrashers, time spent shading by female Gray Catbirds increased much more rapidly with greater exposure of the nest to sunlight.

At a fourth thrasher nest (brood of two young), the parents shaded infrequently when sunlight struck the nest (17 of 1110 min). During nine 30-min intervals, sunlight fell on more than 50% of the nest, but the pair almost never shaded. This nest was completed early in the season before vegetation had entirely leafed out, so it received more direct sunlight than the other three nests, but ambient temperatures were lower. Also, nestlings of the larger

<table>
<thead>
<tr>
<th>Percent of nest in direct sunlight</th>
<th>Number of 30-min observation intervals</th>
<th>Min shading per 30 min (t ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>346</td>
<td>0.8 ± 3.1</td>
</tr>
<tr>
<td>1–25</td>
<td>79</td>
<td>2.3 ± 4.2</td>
</tr>
<tr>
<td>26–50</td>
<td>22</td>
<td>4.9 ± 7.6</td>
</tr>
<tr>
<td>51–75</td>
<td>4</td>
<td>10.3 ± 8.2</td>
</tr>
</tbody>
</table>

*Observations were made at three nests with brood-sizes of three, four, and five young.

<table>
<thead>
<tr>
<th></th>
<th>female</th>
<th>male</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.0 ± 0.1</td>
<td>0.0 ± 0.1</td>
</tr>
<tr>
<td>1–25</td>
<td>0.1 ± 0.3</td>
<td>0.1 ± 0.3</td>
</tr>
<tr>
<td>26–50</td>
<td>0.3 ± 1.3</td>
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<tr>
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<td>2.5 ± 5.0</td>
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<td>2.5 ± 5.0</td>
</tr>
</tbody>
</table>

* Observations were made at three nests with brood-sizes of three, four, and five young.
broods had reduced exposed surface area through which they could dissipate heat, which may have increased the need for shading.

Acknowledgments.—We are grateful to Ellen J. Johnson for laying the groundwork for this study and for assistance in the field. Financial support for this study was provided by the Iowa Agriculture and Home Economics Experiment Station and by Sigma Xi.


Study area and methods.—This study was conducted during the 1980 and 1981 breeding seasons (March–July) within a 24-km radius of Columbia, Boone Co., central Missouri. The 1980 nesting season (April–June) was hot and dry with a total of 15.6 cm (6.13 in) of precipitation, 17.7 cm (6.97 in) below normal (U.S. Dept. Commerce, Climatological Data 84 [4, 5, 6], 1980). The 1981 breeding season was cold and wet with a total of 53.8 cm (21.2 in) of precipitation, 20 cm (8.1 in) above normal (U.S. Dept. Commerce, Climatological Data 85 [4, 5, 6], 1981).

Most breeding pairs were located south and east of Columbia in rolling agricultural areas consisting of a mixture of rowcrops (primarily soybeans), wheat, hayfields, pasturelands, woodlots, and hedgerows. Breeding birds were trapped, using a modified wire-mesh chickadee trap baited with a mouse (Kridelbaugh, N. Am. Bird Bander. 7:50–51, 1982), and banded with a U.S. Fish and Wildlife Service aluminum band on one leg and one or two colored plastic bands on the other. Sixty adults and 120 fledglings were marked during this study. Nests of all breeding pairs were located, and were visited once every 4 days to record data on the nest-site, nesting behavior, nesting habitat, and success. In this paper three terms are used as measures of reproductive success: (1) hatching success—percentage of eggs laid that hatched; (2) fledging success—percent of young hatched that fledged; and (3) nest success—percent of nests from which one or more young fledged.

Arrival and abundance.—Twenty-eight breeding pairs were located in 1980 and 23 in 1981. The average relative abundance of nesting shrikes observed along a 15.5-km route was 0.42 pairs/km. The breeding population in central Missouri is relatively large when compared with other parts of the state (Kridelbaugh 1981). Male Loggerhead Shrikes began arriving in mid-February and established breeding territories. All nine of the wintering birds on the
study area were color-banded and none remained to breed. Likewise, none of the breeding birds or young were known to remain on the study area during winter.

Site fidelity.—Several authors have commented on the high degree of philopatry exhibited by Loggerhead Shrikes (Miller 1931, Bent 1950, Porter et al. 1975). In 1981 54% (15 of 28) of the areas used by nesting birds in 1980 were again occupied. There was a disparity in the fidelity between sexes. Of 15 males banded in 1980, seven (47%) returned in 1981 and set up territories in the same area used the previous year. None of 15 females banded in 1980 returned the following year. In 1980, 90 fledgling were banded on the area. One fledgling (a male) returned and nested 3.75 km from where it fledged. This sexual bias in philopatry was significant ($\chi^2 = 9.1, \text{df} = 1, P < 0.05$) which indicates that in this year males were more faithful to territories of the previous years than were females.

Nest initiation and site selection.—Completed nests were found from 23 March–12 June. Peak nest initiation occurred during late April, with a second peak in late May when color-banded birds renested (Fig. 1). In Illinois shrike nesting peaked in late April (Graber et al. 1973), at higher latitudes in Colorado the nesting peak was in late May (Porter et al. 1975), while in Alabama the peak was reached in early April (Siegel, M.Sc. thesis, Univ. Alabama, Birmingham, Alabama, 1980). In each of these studies, shrikes were one of the earliest nesting passerines in the area.

I observed the construction of nests by three pairs and the time required to construct a nest was 10, 11, and 12 days, respectively. Graber et al. (1973) reported a nest-building period of 5–7 days for two nests which were partially completed when found. The nests were bulky structures made of sticks, with some grass and herbaceous stems, and a lining of cattle hair with some feathers (similar to those described by Bent [1950]). Experienced adult males were first to arrive and establish territories and later led females to potential nest-sites.

Shrikes nested in a variety of trees and bushes. Eastern redecad (Juniperus virginianus) (58%), multiflora rose (Rosa multiflora) (12%), honey locust (Gleditsia triacanthos) (8%), and osage orange (Maclura pomifera) (7%) were used most frequently. Other vegetation nested in included slippery elm (Ulmus rubra), hawthorn (Crataegus spp.), black cherry (Prunus serotina), scotch pine (Pinus sylvestris), and lumbardry poplar (Populus nigra). Sixty-two percent of all nests were along fence lines or hedgerows. Pastureland surrounded 67% of 60 nests, and the remaining nests were located in oldfields (20%), urban areas (6%), hayfields (5%), and a wheat field (2%). Graber et al. (1973) also found redecad, multiflora rose, and osage orange were commonly used by nesting shrikes, but gave no data on the percentage of these nests located in hedgerows. Siegel (1980) reported that Alabama shrikes nested principally in redecad, and 65% of their nests were in hedgerows associated with pastures. In Colorado, Porter et al. (1975) listed elms (Ulmus sp.), willows (Salix sp.), cottonwoods (Populus sp.), and Russian olive (Elaeagnus angustifolia) as support for 70% of all nests. They also found shrikes using grasslands more than cultivated fields. These studies indicate the importance of a dense nesting site (i.e., cedars and thorny vegetation), in open grasslands (i.e., pastures) for breeding Loggerhead Shrikes.

The average height of nests was 3.2 m. Height was significantly affected by the vegetation in which the nest was placed, and was greatest in deciduous trees and lowest in multiflora rose (Kruskal-Wallis test; $\chi^2 = 14.79, \text{df} = 2, P < 0.05$; Table 1). First nests were positioned significantly lower than second nests (Mann-Whitney $U$: $\chi^2 = 9.21, \text{df} = 1, P < 0.05$; Table 1). Nesting success was not affected by nest height ($\chi^2 = 2.63, \text{df} = 1, \text{NS}$). The average height of nests in Alabama was 3.0 m (Siegel 1980), and in Colorado it was 2.2 m (Porter et al. 1975).

Egg-laying and incubation.—Female shrikes layed one egg a day and the clutch-size ranged from 3–7 with most clutches having 5 or 6 eggs (Table 2). The average clutch-size of
shrikes in Florida was 4.38 (N = 16) (Lohrer, M.Sc. thesis, Univ. S. Florida, Tampa, Florida, 1974), in Alabama 5.0 (N = 32) (Seigel 1980), in Illinois 5.68 (N = 134) (Graber et al. 1973), and in northcentral Colorado 6.39 (N = 65) (Porter et al. 1975). Loggerhead Shrikes exhibit a latitudinal cline in clutch-size as do many other species (Spearman correlation, \( r_s = 1, N = 5, P < 0.05; Cody, Evolution 20:174-184, 1966 \)). There was no correlation between clutch-size and date of nest initiation, nor was there a significant difference in the clutch-size in first and second nests (Mann-Whitney \( U; \chi^2 = 0.15, df = 1, NS \)).

I never saw males participating in incubation. This is contrary to what Bent (1950) reported, but agrees with comments made by Siegel (1980). Males fed incubating females on the nest. Shrikes are penultimate incubators (begin incubation with next to last egg), or even antepenultimate in some cases. This results in asynchronous hatching (usually 2 days between oldest and youngest). This difference in age leads to brood reduction during the first week of incubation when environmental conditions are adverse (cold or wet). In 10 nests where one or two young disappeared, the youngest nestlings were gone while the older, larger siblings survived. During the 1980 nesting season (dry and warm) brood reduction occurred at only one nest, while in 1980 (wet and cold) it occurred at nine nests (difference significant, \( \chi^2 = 6.41, df = 1, P < 0.05 \)). At one nest the youngest nestling was found dead in the nest bowl and its stomach was empty suggesting that it starved. At other nests the adults probably removed young before I found them. Adults may remove dead nestlings as if they were foreign material or they may eat them or feed them to surviving young. On three occasions I observed adults canabilizing their own young that had been blown out of the nest and died.

The average incubation period for 13 nests was 17 ± 0.96 days (range = 16–20 days). Miller (1931) reported 16-day incubation period (\( N = 14 \)), Porter et al. (1975) reported an
Table 1

HEIGHT OF NESTS OF LOGGERHEAD SHRIKES IN CENTRAL MISSOURI

<table>
<thead>
<tr>
<th>Height (m)</th>
<th>N</th>
</tr>
</thead>
</table>
| Average (all nests) | 60  | 3.2 ± 2.0 
| Eastern redcedar | 36  | 3.4 ± 2.0  
| Multiflora rose | 7   | 1.1 ± 0.2  
| Deciduous trees | 17  | 3.7 ± 2.0  
| Nest in hedge | 37  | 2.9 ± 1.8  
| Isolated nest | 23  | 3.7 ± 2.3  
| 1st nest | 50  | 2.8 ± 1.8  
| 2nd nest | 10  | 5.2 ± 2.3  

* Paired difference significant (Mann-Whitney U-test, \( P < 0.05 \)).

average of 16 days \( (N = ?) \), and Lohrer (1974) found incubation averaged 16.9 days \( (N = 16) \).

The average number of eggs hatching per nest was 4.9 with an average hatching success of 85.3% (Table 2). Of 36 eggs that failed to hatch, nine were infertile, three had dead embryos, three were lost to adverse weather (blown out of nest), 12 were destroyed by predators (primarily snakes), six were abandoned, and for three the cause of failure was unknown. Hatching success did not differ significantly between years (Mann-Whitney U, NS). In Alabama hatching success was 84.7% (Siegel 1980), and in Colorado (Porter et al. 1975) it was 79.5%. Porter et al. (1975) also found no yearly difference in hatching success.

Nesting and fledging period.—In my study males did not brood the nestlings, but both birds fed the young. The male made more feeding trips to the nest than the brooding female. Both adults participated in nest sanitation by removing fecal sacs and regurgitated pellets. Mean fledging period in 14 nests was 19.1 ± 1.4 days \( (\text{range} = 17-21 \text{ days}) \); Miller (1931) reported 20 days, Siegel (1980) 17.6 days, and Porter et al. (1975) 17 days. Lohrer (1974)

Table 2

COMPARISON OF NEST SUCCESS AND PRODUCTIVITY OF LOGGERHEAD SHRIKES IN CENTRAL MISSOURI, 1980 AND 1981

<table>
<thead>
<tr>
<th>Clutch-size</th>
<th>( t \pm SD )</th>
<th>N</th>
<th>1980</th>
<th>N</th>
<th>1981</th>
<th>N</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. hatching per nest</td>
<td>4.86 ± 1.72</td>
<td>43</td>
<td>4.61 ± 1.90</td>
<td>23</td>
<td>5.15 ± 1.50</td>
<td>20</td>
<td>NS</td>
</tr>
<tr>
<td>Hatching success</td>
<td>85.3%</td>
<td>43</td>
<td>83.5%</td>
<td>23</td>
<td>87.3%</td>
<td>20</td>
<td>NS</td>
</tr>
<tr>
<td>No. fledging per nest</td>
<td>3.04 ± 2.35</td>
<td>53</td>
<td>4.08 ± 2.04</td>
<td>26</td>
<td>2.04 ± 2.23</td>
<td>27</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Fledging success</td>
<td>59.4%</td>
<td>43</td>
<td>77.1%</td>
<td>22</td>
<td>41.9%</td>
<td>21</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Nest success</td>
<td>69.1%</td>
<td>55</td>
<td>82.1%</td>
<td>28</td>
<td>55.5%</td>
<td>27</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

* Mann-Whitney U-test.

\[ \chi^2 \text{ test.} \]
Table 3

Reproductive Success of Loggerhead Shrikes in North America

<table>
<thead>
<tr>
<th>State success, Authority</th>
<th>Nests No.</th>
<th>% success</th>
<th>Eggs Hatched</th>
<th>% success</th>
<th>Fledging No.</th>
<th>% success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alabama, Siegel (1980)</td>
<td>37</td>
<td>43.2</td>
<td>—</td>
<td>84.7</td>
<td>—</td>
<td>50.0</td>
</tr>
<tr>
<td>Colorado, Porter et al. (1975)</td>
<td>65</td>
<td>62.2</td>
<td>5.1</td>
<td>79.5</td>
<td>3.6</td>
<td>55.9</td>
</tr>
<tr>
<td>Illinois, Graber et al. (1973)</td>
<td>20</td>
<td>80.0</td>
<td>—</td>
<td>—</td>
<td>4.6</td>
<td>—</td>
</tr>
<tr>
<td>Illinois, Anderson and Duzan (1978)</td>
<td>13</td>
<td>72.0</td>
<td>—</td>
<td>83.0</td>
<td>3.9</td>
<td>88.0</td>
</tr>
<tr>
<td>Missouri, this study</td>
<td>60</td>
<td>69.1</td>
<td>4.9</td>
<td>85.3</td>
<td>3.0</td>
<td>59.4</td>
</tr>
</tbody>
</table>

* Average per nest.

found that young at nests which were disturbed daily fledged at about 17 days, but not until 19 days from undisturbed nests.

Fledging success in 1981 was significantly lower than in 1980 (Mann-Whitney U, P < 0.05; Table 2). In 1981, frequent storms with torrential rains and cold temperatures occurred just before the young would have fledged resulting in loss of entire broods at eight nests. In 1980 only one nest was lost to severe weather. This difference in nest survival was significant (χ² = 5.58, df = 1, P < 0.05). The dead nestlings had food in their stomachs and probably died from hypothermia. Porter et al. (1975) also found significant yearly variation in the average number fledged (2.2–4.7) and in fledging success (35.8–71.0%). The average number fledged per nest (3.0) and the fledging success (59.4%) found in this study are similar to the results of other studies (Table 3).

I found that after fledging the young remained in the nest tree for 2 or 3 days before flying to other perches and remained dependent on adults for 3 or 4 weeks post-fledging; they then began to forage successfully on their own. This is similar to the findings of Miller (1931).

Also, I found that during the period of dependency the male is abandoned by the female, and thus he must meet the food demands of the fledglings. I observed males “training” their young during this period to recognize potential prey items by drawing them into close proximity with prey, permitting them to make the capture. By 30 June all breeding birds and their young had left the study area except for those that were renesting, and even they had left by 31 July in both years.

Nesting success and renesting.—The average nesting success was 69.1% but it differed significantly between years (χ² = 4.59, df = 1, P < 0.05; Table 2). In 1980 predation was the major cause of nesting failure, but the high winds with heavy rains accounted for 8 of 11 nest failures during the 1981 nesting season. In Colorado, Porter et al. (1975) found significant yearly differences in nesting success (47.8–82.4%). They found that predation accounted for 52% of nest failures, but during the year with lowest success, weather accounted for 67% of the nest failures. Siegel (1980) reported that predation caused 71.4% of nest failures and that the rest were due to abandonment. All studies (Table 3) show that nesting success of Loggerhead Shrikes exhibits great variability from year-to-year, but is relatively high for an open-nesting altricial species in the North Temperate Zone (Nice. Auk 74:305–321, 1957). Therefore, reduced nesting success does not appear to be responsible for the decline of the Loggerhead Shrike in Missouri.

The vegetation in which the nest was placed affected fledging and nest success (Table 4). Nests in multiflora rose had the poorest success, perhaps because they were very low and
TABLE 4
EFFECTS OF VEGETATION ON NEST PRODUCTIVITY AND SUCCESS OF LOGGERHEAD SHRIKES IN CENTRAL MISSOURI (1980–81)

<table>
<thead>
<tr>
<th>Vegetation</th>
<th>Hatching</th>
<th>% success</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(%)</td>
<td></td>
</tr>
<tr>
<td>Multiflora rose</td>
<td>78.6 (6)*</td>
<td>32.4 (6)²</td>
</tr>
<tr>
<td>Deciduous trees</td>
<td>92.1 (11)</td>
<td>75.4 (11)²</td>
</tr>
<tr>
<td>Eastern reededar</td>
<td>85.5 (26)</td>
<td>52.7 (23)²</td>
</tr>
</tbody>
</table>

* Numbers in parentheses are sample sizes.
² Paired difference significant (χ² = 4.82, df = 1, P < 0.05).
³ Paired difference significant (χ² = 7.59, df = 1, P < 0.05).
⁴ Paired difference significant (χ² = 5.18, df = 1, P < 0.05).

provided poorer support (easily tilted by winds). Nest success was highest in deciduous trees, probably due to their thorny nature (Table 1). Siegel (1980) also found success lowest in multiflora rose, and highest in osage orange. There was no significant difference (χ² = 0.04, df = 1, NS) in nesting success between nests in isolated trees and nests in hedges.

Loggerhead Shrikes were considered multibrooded by Miller (1931) and Bent (1950), but Lohrer (1974) found them regularly double-brooded in Florida. No evidence of double brood-
edness was observed in Colorado, although renesting was common (Porter et al. 1975). In Alabama, Siegel (1980) reported that 3 of 20 successful pairs nested again. He also noted that 4 of 11 pairs renested after an initial nesting failure. In the present study 7 of 38 successful pairs (18.4%) attempted a second nest, and 5 of 17 pairs (29.4%) with an initial nesting failure renested. All second nests were build within the original territory. Perhaps some pairs left the study area before renesting. In areas where weather conditions are favorable, and the nesting season is long, shrikes appear to be double brooded (i.e., Florida [Lohrer 1974], California [Miller 1931]). At higher latitudes the number of birds raising a second brood, after a successful initial nesting attempt, declines (Porter et al. 1975).

Acknowledgments.—I express gratitude to W. H. Elder for his valuable comments on the manuscript and for guidance throughout this study, and S. S. Clark for editing assistance. John Faaborg and E. Fritzell read earlier drafts of the manuscript and made helpful comments. This paper is a contribution from the Missouri Cooperative Wildlife Research Unit (School of Forestry, Fisheries and Wildlife, University of Missouri; U.S. Fish and Wildlife Service; Missouri Department of Conservation; Wildlife Management Institute; and Edward K. Love Foundation, cooperating). Partial support was provided by Northeastern Bird-Banding Association.—ALAN KRIDELBAUGH, 112 Stephens Hall, Univ. Missouri, Columbia, Missouri 65211. Accepted 10 Aug. 1982.


Adaptive response of nesting Clapper Rails to unusually high water.—On 13 April 1980, I observed Clapper Rails (Rallus longirostris) respond to high water by building their nest higher. The nest was in Spartina alterniflora in a saltwater marsh in Ocean Springs, Jackson Co., Mississippi. Within 24 h more than 20 cm of rain fell in the area. When the rails were first observed at 09:30 it had just stopped raining. One rail was on the nest, a second, judged to be the male by its brighter orange bill and more distinctive flank and head
markings, was hurriedly adding material to the nest. I watched for 75 min as the male worked—at first hardly leaving the nest to get material, but later moving more than a meter away. He put everything into his efforts, using wings to balance himself, bracing with his feet against live Spartina as he tugged at brown stems, almost flipping over backwards as he rushed material to the nest or to the incubating female. The female moved only to tuck bits under her and to rearrange material around the nest. During a 3-min period, the male made 17 trips to the nest. This rate was maintained for over an hour, and then, when it started to rain again, the male’s pace seemed to quicken but could not be timed because of reduced visibility.

During a lull in the rain I examined the nest. The male retreated 30 m, but the female remained on the nest until I was within 0.6 m, at which point she stepped to the rim of the nest to reveal her nine eggs. The water in the marsh was rising and near the nest rim so I retreated.

On 21 April I found the female still incubating nine eggs and equally tenacious. There had been little rain since 13 April and the water level in the marsh had dropped to 41 cm below the nest rim. On the 21st the nest measured 19.5 cm deep (from rim to bottom) and 31 cm across. The diameter of the enlarged nest (31 cm) exceeded the largest Clapper Rail nest (30.5 cm) $\bar{x} = 23.6$ cm, $N = 63$ reported by Kozicky and Schmidt (Auk 66:355–364, 1949), suggesting that enlargement may have been outward as well as upward.

Several authors (e.g., Bent, U.S. Natl. Mus. Bull. 135, 1926; Adams and Quay, J. Wildl. Manage. 22:149–156, 1958) recognized high tides and floods as threats to Clapper Rails. None mentions a response to rising water as observed in this case. Zucca (Wassman J. Biol. 12:135–153, 1949) observed 12 nests during 3 days of high tides; several nests were lost, some damaged, all were soaked, but no mention was made of nest enlargement. Meanley (N. Am. Fauna No. 69:60, 1969) observed a King Rail (Rallus elegans) build up its cattail nest above rising water in a roadside ditch and another building its nest up when the rice field in which it was located was flooded. Both of these nests were built up by single incubating birds working from the nest.

Lack of previous observations of this type of behavior in Clapper Rails is probably due to the wave action which usually accompanies high tides and which would thwart nest reinforcement activity. The extreme, but gentle rise in water level in this instance put little disruptive stress on the nest and allowed the bird to work without fighting waves or a strong current. My observation that the gathering of nest material and most of the nest reinforcement activity was done by the male also parallels Meanley’s (1969:60) observations of nest construction by male King Rails.—JEROME A. JACKSON, Dept. Biological Sciences, Mississippi State Univ., Mississippi State, Mississippi 39762. Accepted 13 July 1982.


Chick movements in Common Poorwills.—Common Poorwill (Phalaenoptilus nuttallii) chicks are reported to move frequently during the nestling stage. Evans (Wilson Bull. 79:453, 1967) re-examined a poorwill nest in Nevada six times and noted five changes of site involving moves from 2.1–10.6 m. In Oregon, Swisher (N. Am. Bird Bander 3:152–155, 1978) noted that a brood moved 1 m, then returned to the original nest-site and then apparently left the nest area. Orr (Auk 65:46–54, 1948) found that 1–2 day-old undisturbed chicks moved 0.15 m to cover.

In 1981 we recorded moves of a poorwill brood in the Rosebud Buttes, 12 km SE Rosebud, Rosebud Co., Montana. The area was dominated by ponderosa pine (Pinus ponderosa) and Rocky Mountain juniper (Juniperus scopulorum).
On 6 and 7 June we flushed an adult from two eggs located on the ground on pine needles between a scrub juniper and a yucca (Yucca glauca). On 14 June an adult was flushed from two downy chicks at the same site. An adult was flushed on 24 June from the chicks, which were 2.5 m east of the nest-site and in the shade of a large juniper. Distribution of droppings indicated that the chicks had remained in an area of 1.5 m² since hatching. The maximum distance moved was 3.1 m. During this visit we banded the chicks—the first handling of eggs or chicks. On 26 June we flushed an adult from the chicks next to a large juniper 14.5 m west of the 24 June location. The chicks were weighed and measured. We could not relocate them on 5 July.

There appear to be two types of chick movements. Short movements may be a thermo-regulatory response, e.g., avoiding wet areas (Swisher 1978) or too much sunlight, as reported for Common Nighthawk (Chordeiles minor) chicks (Dexter, Bird-Banding 23:109–114, 1952; 27:9–16, 1956). Movement to nearby cover may also constitute concealment from aerial predators. Long movements may be an anti-predator adaptation (Dyer, Wilson Bull. 89:476–477, 1977) triggered by disturbance. Long movements reported by Evans (1967) and Swisher (1978) both followed handling of chicks. Consistent with this, the chicks we observed moved to denser cover and remained within 3.1 m of the nest-site for 10+ days posthatching, but made two long movements following handling.


Adoption of introduced young and neglect of own by nesting Black Vultures.—On 7 June 1975, I learned of the planned demolition of an old house used by a nesting pair of Black Vultures (Coragyps atratus). The nest contained one young bird, 35–40 days old. At the same time a pair of Black Vultures were nesting in an old building on my farm, having two young, 30–35 days old. With the hope that the parent birds at this nest would adopt and feed the young bird from the other nest along with their own, I placed the bird from the other nest with the two birds in the nest on my farm. In addition to noting the slightly larger size, I clipped a toenail to facilitate identification of the introduced bird. Through a peep hole I watched the Black Vultures feeding the nestlings and found that the introduced bird was accepted by the adults and was being fed by them. Thus, I anticipated no problem with the introduction and did not visit the nest again for 3 days. Then I found the smaller of the two original birds much emaciated and nearly dead, apparently from starvation. This bird died and I removed it from the nest the following day. Neither the other young nor the adults had made any attempt to eat the dead chick. The two remaining young were well fed and healthy.

I earlier reported (Stewart, Auk 91:595–600, 1974) finding Black Vultures holding their eggs on the inner and central toes of their feet during incubation, setting at two the maximum number of eggs which can be incubated. The observation reported here of feeding being limited to two birds indicates that the limitation of two is continued beyond incubation. It seems probable that this limiting to two the number of young fed is an outgrowth from the method used by these birds for incubating their eggs. Perhaps from being able to incubate only two eggs and thus having only two young they develop a tendency to feed only two young.
This pattern of feeding being restricted to two nestlings may have resulted from the need for restricting demands on available food supplies and thus competition for food among nestlings. This is suggested by the fact that selective feeding favored the larger birds. However, competition for food among the nestlings is not now the effective operating principle restricting the brood-size of Black Vultures to two birds. I believe the two birds could not have demanded the full time of the adults for their feeding, unless the third bird was excluded from feeding by the selective feeding of the adults and thus it should have received some food and not died so soon. Also, I earlier found (Stewart 1974) that parent Black Vultures normally initiate feeding and that individual young birds await an opportunity to be fed. The selective feeding practiced thus appears to be a behavioral adjustment associated with the number of young birds to be fed and not the excessive demand on the food supply. Acceptance of the introduced bird and neglect of the smaller of their own nestlings by the pair suggests that larger size instead of kinship elicited preferential treatment from the parent birds.—Paul A. Stewart, 203 Mooreland Dr., Oxford, North Carolina 27565. Accepted 1 Aug. 1982.

Wilson Bull., 95(2), 1983, pp. 311–313

Malformation of the oviduct in a Canada Goose.—After pair formation and nest construction, failure to lay followed by incubation behavior on an empty nest is a rare phenomenon in wild birds. Heusmann and Peikkala (Wilson Bull. 88:148–149, 1976) recorded such an example in a Wood Duck (Aix sponsa) and Fjætland (Wilson Bull. 90:456–457, 1978) and Lumsden (Wilson Bull. 92:415, 1980) each reported a case in a Canada Goose (Branta canadensis). Male (Br. Birds 70:394, 1977) recorded a Great Tit (Parus major) incubating in an empty nest, and Kettle (Br. Birds 71:12, 1978) reported a similar incident involving a Blue Tit (Parus caeruleus). Dhondt and Eyckerman (Br. Birds 71:600, 1978) found 7 of about 1000 pairs of Blue Tits and 2 of about 1500 pairs of Great Tits incubating empty nests on their study areas around Ghent, Belgium. In these examples the cause of failure to lay was not determined. We here discuss the causes of failure to lay in a Giant Canada Goose (B. c. maxima).

The nesting behavior of a wild Giant Canada Goose was recorded from 1976–1978 when she annually built nests but did not lay (Lumsden 1980). This female was banded F13 as an after-hatching-year bird, and returned with the same mate to nest at the same location for 3 consecutive years. When given fertile eggs she incubated, hatched, and raised goslings.

In 1979 this female built a nest by 25 April, but still had not laid eggs by 22 May. When given dummy eggs, she incubated steadily until 21 June, but later deserted.

In 1980 her nest was built by 9 April and she was sitting steadily by 26 April. By 9 May she had not laid and was given dummy eggs which she incubated for 61 days until 26 June, when she deserted.

On 14 April 1981, F13 and her mate returned to the nesting island and began to prepare a nest-site. By 24 April she had completed a new nest lined with a small quantity of down and was given dummy eggs. On 26 April she started to sit continuously and on 27 April her nest contained an abundance of down. In Canada geese some down is usually present in the nest when the penultimate egg is laid and when the last egg in the clutch is laid an abundance of down is shed into the nest. It was decided to collect the female and ascertain what was responsible for the inability to lay eggs, yet manifest normal reproductive behavior. The collection of this 7-year-old bird was timed to coincide as closely as possible with the time when the last egg could be expected to be laid. The carcasses of F13 and her mate were frozen immediately and stored for study.
Body condition of F13.—In 1981, as in previous years, this goose fattened normally (Hanson, Arctic Inst. Tech. Paper No. 12, 1962), and by late April, had reached the “rounded” abdominal profile class 3 (Owen, J. Wildl. Manage. 45:227-230, 1981). Giant Canada Geese of this southern Ontario population (Lumsden, Ont. Field Biol. 35:49-56, 1981) do not acquire the massive fat loads of more northern breeding stocks (Mainguy et al., unpubl.) and probably seldom achieve the sagging class 4 abdominal profile. The live weight, mass of the pectoralis major and supracoracoideus muscles, weight of the empty gizzard and heart, and weight of the abdominal fat depot conformed to the values encountered in wild Giant Canada Geese breeding along the Toronto waterfront 55 km to the south. The liver weight fell within the normal range for breeding geese and showed signs of lipid accumulation (Mainguy, M.Sc. thesis, Univ. Guelph, Guelph, Ontario, 1982).

The ovary.—The ovary was without sign of disease or deformity and appeared normal for a goose killed at that stage of the breeding cycle. There was one yellow follicle, smooth, firm, and round, apparently still under rapid yolk development. This weighed 4.4 g or about 7% of the weight of an average yolk from an egg of this goose population. This follicle was probably destined to be resorbed, because to attain maturity, it would have had to undergo about another 6 days of rapid yolk synthesis (Lumsden, unpubl.). The abundance of down in the nest suggested that her laying cycle was completed 1 or 2 days before collection. There were six well-defined atretic follicles heavily vascularized with wrinkled, flaccid pinkish-grey walls. These weighed sequentially, 3.2, 1.3, 0.8, 0.2, 0.1, and 0.07 g. Also present were numerous small follicles of the normal size for ova in the resting stage. Ovulated follicles were not present.

The oviduct.—The oviduct and the entire cloacal region when dissected from the carcass, revealed that the oviduct structure was grossly deformed (Fig. 1). The oviduct weight was 21.7 g compared to $83.7 \pm 3.27$ g ($N = 18$) in a normal goose during the laying period. The

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**Fig. 1.** Deformed oviduct of a Giant Canada Goose lacking an infundibulum.
exit from the oviduct into the cloaca was open. Since this bird could never have laid an egg, the oviduct likely opened by hormonal means.

The lumen appeared normal, and no tumor or polyp was present. The exit from the lumen was tied off with thread at its junction with the cloaca and inflated with air by means of a pipette. It was apparent that the isthmus was blocked, because no air passed into the magnum. The magnum was grossly foreshortened and a further constriction was present at its anterior end. This constriction was also blocked and prevented the passage of air. When the magnum was punctured for the injection of air, a quantity of pink viscous (albumen?) material flowed out. Anterior to the upper blockage the oviduct was narrow, 27.7 mm long, ensheathed in peritoneal tissue and terminated in a point. The funnel-shaped infundibulum was missing. The failure to lay in this goose was clearly a result of a deformed and blocked oviduct.

It is of interest that the ovary which appeared to be normal contained six atretic follicles, but no indication of ovulated follicles. These atretic follicles were graded in size indicating that at maturity each in turn began to resorb. If the endocrine system as a whole had been functioning properly we would expect that ovulation would have taken place, but into the body cavity, since the infundibulum was missing.

Cole and Hutt (Poult. Sci. 32:481–492, 1953) described a condition in 26 of 324 fowl in which the cause of non-laying was an incomplete oviduct. They stated that in most of these the infundibular portion of the oviduct persisted, while a section of the albumen secreting region degenerated. They did not specifically discuss the state of the ovaries in these birds and nowhere described the presence of atretic follicles. In their discussion of non-layers with normal oviducts they noted there was often liquid yolk in the body cavity indicating that the bird had ovulated but the yolk had not been picked up by the infundibulum.

Failure to ovulate suggests a deficiency of LH, and atresia is controlled by the secretion of progesterone (Van Tienhoven, Endocrinology of Reproduction in Birds, pp. 1088–1169. in Sex and Internal Secretions, W. C. Young, ed., Williams and Wilkins, Baltimore, Maryland, 1961). It seems likely that the massive deformity of the oviduct of the Giant Canada Goose F13 probably occurred during early ontogeny. We speculate that the deformity and the absence of the infundibulum may have prevented adequate secretion of LH, hence the absence of ovulated follicles. However, adequate secretion of sex hormones occurred to allow copulation, pair-bonding, nest-building, incubation, brooding behavior, and presumably five seasonal proliferations and regressions of the oviduct. The development of the magnum and the presence of gelatinous material suggests that this zone of the oviduct, although reduced in size, was still able to respond to the synergistic effects of estrogen and progesterone. This is Ontario Ministry of Natural Resources, Wildlife Research Contribution No. 82-05.—HARRY G. LUMSDEN, Ontario Ministry of Natural Resources, Wildlife Research Section, P.O. Box 50, Maple, Ontario L0J 1E9, Canada; AND VERNON G. THOMAS, Dept. Zoology, Coll. Biological Science, Univ. Guelph, Guelph, Ontario N1G 2W1, Canada. Accepted 15 Sept. 1982.

Wilson Bull. 95(2), 1983, pp. 313–314

Black-capped Chickadee performs “hiss-display” while in wire-mesh trap.—On 15 July 1981, I re-trapped a color-banded female Black-capped Chickadee (Parus atricapillus) that had visited feeders in my yard in Logan, Cache Co., Utah, intermittently between her initial capture on 13 December 1980 and 21 April 1981. The bird was not re-trapped during that interval. I carried her into the house (a distance of 11 m) in the wire mesh trap 17 × 17 × 16 cm. As I placed the trap on the table the chickadee, which crouched on the
floor of the cage facing away from me, extended her wings quickly, thumping the floor of the trap while simultaneously making a hiss-like vocal sound that I transliterated as *haaah*. A single repetition of the display followed immediately.

The "hiss-display" (Gompertz, Vogelwelt 88:165-169, 1967) usually is elicited when an incubating titmouse (*Parus* sp.) is disturbed in the nest cavity. Components include rising on the tarsi, thrusting the head forward while expelling air, opening the wings rapidly to strike the walls of the cavity, and spreading the tail. Several postures of a sequence in the Great Tit (*P. major*) are illustrated in Gompertz (1967) and the sound spectrogram in Fig. 2 of her paper demonstrates that the wing-strike immediately precedes the hiss. This display has been reported in *P. atricapillus* by Burleigh (Auk 47:48-65, 1930) and Odum (Auk 58: 518-535, 1941).

Löhr (J. Ornith. 105:153-181, 1964) noted that this "threat combination" was fully elicited only in a cavity, but that males performed it in nest defense and titmice in roost holes at night also hissed when the observer scratched the trunk outside the opening. Löhr also observed the display regardless of season in injured titmice that were startled at the opening of the carton in which they were enclosed.

The confinement in a small space that afforded no escape route, and the proximity of my hands on the sides of the trap evidently elicited a response normally given only when titmice occupying unlighted cavities are disturbed.—KEITH L. DIXON, Dept. Biology and the Ecology Center, Utah State Univ., Logan, Utah 84322. Accepted 8 July 1982.


On 20 July 1981, Carl Swafford, Chuck Arellano, and I saw an Orange-breasted Falcon in the western part of Cayo District, Belize (16°49'N, 88°59'W) between 500 and 600 m elev. The bird was perched in the top of a partially defoliated palm (probably *Orbigyna cohune*) in a small clearing 9 km south of the crossing by the road from Augustine to Millionario of the Rio Guacamayo, a tributary of the Belize River draining the western slope of the Mountain Pine Ridge and Mayan Mountains.

The bird was not disturbed by our approach on foot and we obtained an excellent view in full sunlight through 7× binoculars from distances less than 25 m. We noted the white throat contrasting with a rufous-orange breast, a rufous-orange, partial neck collar and lower belly, black and buffy-barred lower breast and upper belly, and blackish back, wings and upper head. Direct comparison with the similar, though smaller, Bat Falcon (*Falco rufigularis*) was made possible by the presence of an individual of that species which made several aerial passes at the Orange-breasted Falcon while uttering a shrill, kestrel-like *kree*. The Orange-breasted Falcon made no response other than lowering its head slightly and was still on the same perch 2 h later when we retraced our route. At that time it held in its talons a small bird which we were unable to identify.

This section of Belize is remote and sparsely inhabited, the few residents having been relocated as a result of the dispute with Guatemala. Annual rainfall of 2000-4000 mm supports a tall wet forest which Russell (1964) referred to as Tropical Moist Forest Life Zone
from the Holdridge scheme. Orange-breasted Falcons are known to nest and occur regularly at Tikal National Park, Guatemala (Smithe, The Birds of Tikal, Natural History Press, Garden City, New York, 1966; pers. obs.) 70-80 km to the northwest.

I thank Amadeo M. Rea and Stephen M. Russell for their comments on this note.—J. CHRISTOPHER HANEY, Dept. Zoology, Univ. Georgia, Athens, Georgia 30602. Accepted 13 July 1982.

Wilson Bull., 95(2), 1983, p. 315

First record of the Little Egret (Egretta garzetta) in Suriname.—On 3 June 1969, a small white heron was shot in the Saramacca District of Suriname, South America, west of Paramaribo (5°57'N, 55°12'W). The bird bore a band inscribed “Aranzadi, San Sebastian, Espana H 15 215.” The hunter brought the bird to the Surinam Forest Service where the inscription and the number of the band was transcribed. Unfortunately, neither the bird nor remnants were preserved, as the Forest Service refused to pay the price asked for the bird.

According to the San Sebastian Banding Office, the bird was a Little Egret (Egretta garzetta) banded as a nestling at Doñana, Huelva Province, Spain (37°N, 6°27'W) on 11 June 1968. This record is the first for this Old World species on the mainland of South America and the fifth record in the New World. The others are: (1) Conception Bay, Newfoundland, Canada, on 8 May 1954 (specimen in National Museum of Natural Science, Ottawa) (Godfrey, Auk 73:457, 1956); (2) Barbados, West Indies, on 16 April 1954 (specimen in Peabody Museum, Yale University) (Bond, 11th Suppl., Birds of the West Indies, 1966); (3) Trinidad, West Indies, on 13 January 1957, banded as a nestling on Doñana, Spain, on 24 July 1956 (Downs, Auk 76:241, 1959); and (4) Martinique, West Indies, on 6 October 1962, also banded as a nestling on Doñana, on 24 July 1962, (Bernis, Aves Migradoras Ibericas. Publ. especial de la sociedad Espanola de Ornitologia 1, 1966).—F. Haverschmidt, 16 Wolfskuilstraat, 7731 At Ommen, Holland. Accepted 15 Oct. 1982.
ORNITHOLOGICAL LITERATURE

Species Limits in the Indigobirds (Ploceidae, *Vidua*) of West Africa: Mouth Mimicry, Song Mimicry, and Description of New Species. By Robert B. Payne. Misc. Publ. Mus. Zool. Univ. Mich. No. 162. 1982. 96 pp., 29 figs., 5 tables. Price not given.—In the indigobirds of southern Africa, male plumage is a blackish color with green, blue or purple gloss. Females of all species have streaked “sparrowy” brown plumage. Males of similar morphological type in a given area mimic the song of a single species of firefinch (*Lagonosticta*) on which the female indigobirds are brood-parasitic, and there is a high degree of assortative mating as females tend to mate with males having bill and foot color similar to their own. It is therefore possible to determine nonarbitrary species limits in this complex of morphologically similar forms.

The situation in West Africa is less clear, however, because while males vary in plumage color, female indigobirds seem to be indistinguishable, and some criterion other than that of assortative mating must therefore be found for determining species boundaries for coexisting populations of indigobirds. Payne and others have found in earlier studies that young indigobirds mimic the mouth pattern of the young of their host firefinch species. Because this is a genetically determined trait rather than an acquired one, it could be a useful means of distinguishing local populations of indigobirds. In the present study Payne used this criterion to establish the occurrence of genetic differences among the indigobirds associated with different species of firefinch hosts, and further looked for association in indigobirds of distinct male breeding plumage and mimicry of a single firefinch species’ song. By applying these two criteria Payne was able to determine with considerable confidence the limits of five species of *Vidua* in West Africa, including *V. raricola* and *V. larvaticola* spp. nov.; these latter two had previously escaped attention because of morphological similarity to other forms. A thorough discussion of the abundant nomenclatural problems is given as well as maps showing distribution of the indigobird species and their firefinch hosts, sonagrams, photographs of nestling mouth patterns and a very useful gazetteer.

In cases of disjunct populations Payne primarily used song mimicry to link these populations with known species of indigobirds: they were considered conspecific with species A if they mimicked the same firefinch song as A even if they were morphologically dissimilar to A. In general, all indigobirds that mimic the song and the mouth pattern of nestlings of a single species of firefinch were considered members of a single species of *Vidua* regardless of geographic occurrence and external adult morphology. Males singing the same mimetic song in a local area tend to be similar in breeding plumage, however.

It is possible to identify most museum specimens of male indigobirds taken in the areas studied intensively even when nothing is known about the song behavior of the birds prior to collection. This is not true of females, however, and specimens from areas where little field work has been done are best left nameless until further studies of indigobird behavior and morphology in such areas clarify species relationships.

Although the species concept most widely accepted at present is the biological one, that interbreeding organisms constitute a single species, it is frequently impractical to apply this concept in determining species limits, and some form of the morphological species concept is most commonly applied. Indigobirds generally resist the application of both concepts, however, and Payne’s extensive field work and careful analysis have resulted in an approximation that is both more appropriate to and revealing of the unusual biology of his animals.—MARY C. MCKITRICK.
BIRD POPULATIONS IN EAST CENTRAL ILLINOIS: FLUCTUATIONS, VARIATIONS, AND DEVELOPMENT OVER A HALF-CENTURY. By S. Charles Kendeigh. Illinois Biological Monograph No. 52. Univ. Illinois Press, Champaign, Illinois, 1982: 137 pp., 32 text figures, 10 tables, 4 appendices. $14.50.—Long-term studies of bird populations hold a special place in modern ornithology because so few researchers have had the opportunity or persistence to amass such records and because of the obvious value such studies have in understanding the dynamics of the studied populations. As rare as long-term population studies are, long-term studies of entire bird communities are ever rarer, and continuous uniform records spanning as many as 50 years, such as Kendeigh presents in this monograph, are nearly without precedence.

The major value of this unique volume may be that it presents in tabular form so many data in such straightforward and easily interpreted ways. Breeding birds of seven forests (a habitat restriction not alluded to in the title) were censused by spot-mapping, and winter populations were indexed by counts over known distances (Christmas bird counts) or known areas. The close agreement over the years of these three population estimates is interesting to note.

In addition to presenting the results of these population estimates in species-by-species accounts, Kendeigh interprets the year-to-year variations and fluctuations within the bird communities with respect to several environmental changes that took place on the study area: maturation of forests, succession, loss of elms to disease and the resulting temporary flush of wood-boring insects, range expansions and contractions, and local extirpations. These interpretations are cautious, and the monograph is free of much of the speculation that usually accompanies explanations of complex population fluctuations. On a few points, however, Kendeigh may have been too cautious. His brief discussion of how his results relate to the current puzzle over the declines of many forest-dwelling neotropical migrants seems very superficial, in view of the obvious relevance of his data.

Kendeigh’s study areas are isolated stands of forest in an agricultural landscape and so should be of special interest to island zoogeographers who have rarely had such a complete data set with which to play. Many ornithologists will be curious to see how the particular species or group that they study has fared over the past 50 years in Illinois. Others who may make use of the data will be grateful for Kendeigh’s foresight and perseverance in compiling such a unique record.—STANLEY A. TEMPLE.

THE BARN OWL. By D. S. Bunn, A. B. Warburton, and R. D. S. Wilson, illus. by Ian Willis. Buteo Books, Vermillion, South Dakota, 1982:264 pp., 31 photographs plus one color frontispiece, all captioned, 11 numbered text figures, 39 tables. $32.50.—Of the total number of pages of this book, 6.0% are allotted to introductory material (including a preface), 10.6% to “Description of adaptations,” 3.4% to “Voice,” 10.2% to “General behaviour,” 8.7% to “Food,” 16.7% to “Breeding,” 6.8% to “Movements,” 11.0% to “Factors controlling population, and possible conservation measures,” 12.9% to “Distribution in the British Isles,” and 5.3% to “Folklore.” The remaining 8.4% is made up of three appendices, a list of references, and an index. There is a surprisingly small number of typographical errors and mistakes, and most of these correspond to misspellings of taxonomic entities (e.g., Scarp-bacidae, Accipiterinae, Charidriformes, P. duodecimeostatus). In the first paragraph on p. 105, a contradiction can be found between the statement in the text and the results referred to in Fig. 6 (p. 106). Table 33 is mistakenly referred to in the text as Table 34 (p. 163), and the reference to the real Table 34 is missing (p.164). Two instances of antiquated taxonomy are found in Appendix 1 (Citellus for Spermophilus, and P. ctenifer for P. melanoleucus).
No statistical treatment has been given to the results in any of the tables, and the most sophisticated statistics to be found are percentages, medians, and means (without associated dispersion statistics). A wealth of raw data is spread throughout the book.

On the dust jacket, it is said that this book is “... a detailed, balanced account based on intimate knowledge of the Barn Owl in varying habitats in Britain, comparing, as appropriate, this race’s behaviour with that of sub-species in other areas of the world.” I agree with the first part of the statement. Throughout most of the book I was impressed with the very detailed account of the several aspects of the behavior of British Barn Owls (Tyto alba alba). I found the chapters on voice (#2), general behavior (#3), breeding (#5), and movements (#6) to be the best. Both the introductory chapter (#1) and that on food (#4) are of somewhat lesser quality, though in this latter case I may be biased in my judgement because my own competence is with this aspect of owl biology. Chapter 7 becomes rather amusing when one reads that among the major factors controlling British Barn Owl populations are “Unorganised shooting and game keeping” and “Taxidermy.” In this same chapter several other ecological factors are considered, and on the average it is a very interesting one to read. Chapter 8 deals with population status and historic trends of the Barn Owl in the British Isles, and I think that the overly detailed accounts presented in there (on a county by county basis!) should have not been included in the book because of their mainly local interest. The last chapter (#9) on folklore I found of limited interest and unnecessary. Appendix 2 “Development of young Barn Owl” is very informative, and Appendix 3 “Watching the Barn Owl” gives some interesting hints on conducting behavioral observations of this bird. What I miss the most is a chapter dealing with the ecological place of the British Barn Owl in the context of the local assemblage of owls. The treatment of the Barn Owl in this book is strictly autecological, and knowing that so much has been done on other British owls I would have liked to see a general and summary comparison between them and the subject of this book.

Regarding the promised comparisons of the natural history of T. alba alba with that of the other subspecies in the world (see quotation of flap cover above), I must say that they are biased and not very extensive. Most of the comparisons are made to the continental European T. alba guttata, and to the North American T. alba pratincola. This situation is perfectly reflected in the references listed. Of the 218 titles cited, 51.8% correspond to work done in Britain, 22.5% correspond to North American publications, 19.3% to work done in continental Europe, South America, Africa, and Asia, altogether account for only 6.4% of the references listed. No paper is cited from the good work being done in Australia. In the preface (p. 14) it is said that “Whilst D.S.B. and A.B.W. were searching for subjects to observe, Robert Wilson was combing diligently through the literature for helpful references ...” Apparently, Wilson did a good job in reading the British and continental European literature (there are references up to 1979 and 1980), but his readings of the North American literature did not keep pace with the local production (the most recent reference is from 1977). I am not thoroughly familiar with the African and Asian Barn Owl studies, but it seems to me that something has to have been done since 1970–1972 (the most recent dates in the bibliography). The only reference cited from South America is dated in 1962, but I am aware of at least two papers published in a major U.S. ornithological journal during 1979–1980, and of one published in 1976 in a European journal. Perhaps these criticisms sound too harsh, considering that the Barn Owl is perhaps the most studied single species of owl in the world, and that there are hundreds of research papers scattered through many obscure journals. However, with the publication of “Working bibliography of owls of the world” by Clark, Smith, and Kelso (1978), ignorance of the relevant literature is not a good excuse anymore.

The main point I wish to make here is that a broad-based comparison of the natural history
of the Barn Owl in different parts of the world is still missing and is badly needed. This book provides a very detailed data baseline on one of the ±35 Barn Owl subspecies, but unfortunately it runs short of making a thorough comparison with even the other two best known subspecies (T. a. guttata and T. a. pratincola). A definitive treatment of the Barn Owl on a world basis has not come out yet, but I think that this book is a good and encouraging step toward that aim. It is on this basis that I do not hesitate to recommend it to all researchers working on this bird.—FABIAN M. JAKSIC.


ORNITHOLOGICAL NEWS

BIRD BANDING RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering research grants of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her banding or ornithological background, the project plan, and a budget to the Joint Selection Committee Chairman: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. Deadline for applications is 15 March 1984.

HAWK MOUNTAIN RESEARCH AWARD

The Hawk Mountain Sanctuary Association is accepting applications for its fifth annual award for raptor research. To apply for the $500.00 award, students should submit a description of their research program, a curriculum vita, and two letters of recommendation by 30 September 1983. to James J. Brett, Curator, Hawk Mountain Sanctuary, Route 2, Kempton, Pennsylvania 19529. The Association’s Board of Directors will make a final decision late in 1983.

Only students enrolled in a degree-granting institution are eligible. Both undergraduate and graduate students are invited to apply. The award will be granted on the basis of a project’s potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.
NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society provides grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants totalling $3,000.00 are available consisting of varying amounts; generally stipends of $1,000.00 are awarded.

*Student Research Grant.*—Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

*Bluebird Research Grant.*—Available to student professional or individual researchers for a suitable research project focused on any of the three species of bluebirds from the genus *Sialia*.

*General Research Grant.*—Available to student, professional, and individual researchers for a suitable research project focused on a North American cavity nesting species.

Further guidelines and application forms are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 66, Upham, North Dakota 58789. Completed applications must be received by 31 January 1984; decisions will be announced by 15 March 1984.

NATIONAL WILDLIFE REHABILITATION ASSOCIATION CONFERENCE

The third annual conference of the National Wildlife Rehabilitation Association will be held at the Kalamazoo Nature Center in Kalamazoo, Michigan, 22–26 February 1984. Persons interested in presenting papers on animal rehabilitation, aspects of veterinary medicine, fund-raising or public education as related to Wildlife, optimum caging related to holding and release of wildlife, or natural history and life cycles of wildlife species as related to rehabilitation should submit abstract, handouts, and autobiographical sketch to Patricia Adams, Program Chair, National Wildlife Rehabilitation Conference, % Kalamazoo Nature Center, 7000 North Westnedge Ave., Kalamazoo, Michigan 49007. Deadline is 15 October 1983. Symposium Proceedings will be published.

This issue of *The Wilson Bulletin* was published on 27 July 1983.
SUGGESTIONS TO AUTHORS


Manuscripts intended for publication in The Wilson Bulletin should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Checklist (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411-419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, New York 14850.

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MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.
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ORNITHOLOGICAL NEWS
THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

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THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museum, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for The Wilson Bulletin. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library’s holdings was printed in the September 1952 issue of The Wilson Bulletin and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN

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All articles and communications for publication, books and periodicals for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication OSNA, Council Laboratories of Ornithology, 195 Sherman Woods Rd., Ithaca, New York 14850.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.
Adult male Band-tailed Manakin, *Pipra f. fasciicauda* from an acrylic painting by F.P. Bennett, Jr.
THE DISPLAY REPERTOIRE OF THE BAND-TAILED MANAKIN (PIPRA FASCHICAUDA)

MARK B. ROBBINS

The diversity of mating systems in Neotropical birds is impressive. One family, the manakins (Pipridae), is particularly rich in mating systems; nearly the full gamut is represented among its 51 species (Snow 1979), with most species being promiscuous (Snow 1963b, Sick, 1967). This promiscuity, with its congregations of brightly colored males at leks, is considered to represent the most highly derived type of mating system (Lack 1968). Presumably, a gradual shift in diet from insectivory to frugivory, emancipating males from nesting duties (Snow 1963b), coupled with the nondefensibility of either resources or female groups may have pre-adapted manakins for evolving a lek mating system (Emlen and Oring 1977, Bradbury 1981). Recently, Bradbury (1981) suggested that the crucial selective force in developing lek behavior (given the above conditions) is an increase in female home-range size relative to the size of existing male territories. This may lead to a shift in male strategies from resource defense to self-advertisement and with female preference for clustered males will lead to congregations of displaying males at localized sites within a habitat (Bradbury 1981).

Although something is known about the courtship behavior of nearly half of the manakins (Snow 1963b, Sick 1967), many have yet to be studied. Due to apparent rapid evolution in this group (Schwartz and Snow 1978), different populations of a species may exhibit unique morphological and behavioral characteristics that make it necessary to study each species under a variety of conditions within its range (Sick 1967).

Although the Band-tailed Manakin (Pipra fasciicauda) is relatively widespread throughout southern Amazonia (Snow 1979), little information exists about its natural history (Sick 1967, Schwartz and Snow 1978). On the basis of morphology and zoogeography, the band-tail is closely related to
the Wire-tailed (*Pipra filicauda*) and the Crimson-hooded (*P. aureola*) manakins; these three species are thought to comprise a superspecies (Haffer 1970). The purpose of my study was to elucidate the display repertoire of *P. fasciicauda* and to compare its behavior with that of the other members of the superspecies complex.

**STUDY AREA AND METHODS**

The study was carried out in the Tambopata Natural Wildlife Reserve, near the mouth of the Rio La Torre (=Rio D’Orbigny) on the south bank of the Rio Tambopata in the Department of Madre de Dios, Peru (12°50'-55'S, 69°17'W) between early June and mid-December 1980. The study site is situated in undisturbed lowland rain forest at about 260 m elevation. The mean annual rainfall is estimated to be 1500-2000 mm and the mean annual bio-temperature to be between 18°C and 24°C (Hartshorn 1979). Puerto Maldonado, ca. 25 km NNE of the study site, averages 1897 mm of rain annually (Oficina Nacional de Evaluación de Recurso Naturales 1976). Relatively little rain fell on the study area from June to mid-September 1980. Rain and strong winds accompanied cold fronts, locally known as "friajes," from the south every 6-10 days throughout the above period. With the arrival of these cold fronts, temperatures often dropped from about 27°C to near 10°C in just a few hours. By late September storm systems were mainly from the NNE. Rainfall gradually increased through the remaining 3 months of the study.

All five leks visited were in seasonally flooded forest. Apparently, *P. fasciicauda* is restricted to this type of forest (J. V. Remsen and T. A. Parker, unpubl.). The study was concentrated at a single lek that has persisted since at least 1977 (T. A. Parker, pers. comm.). The lek area is transected by several meandering streams that fill at the height of the rainy season (January-mid-March). A stream channel that empties into the Tambopata River dissect the northern end of the area. This stream is completely dry from May-September, with small pools persisting during the early wet and dry seasons. The strong winds associated with the friajes often felled many trees and innumerable limbs. The felling of trees combined with the scant vegetation in the canals created large light gaps in the study area. As a result, the undergrowth (0–5 m) was dense, consisting primarily of melostomes (*Miconia* spp.; Melostomaceae), small palms (*Palmaceae*), and a number of epiphytic vines (Araceae). Small stands of bamboo (*Guadua* spp.) were scattered throughout the area. Palms were a common and conspicuous element of the middle and upper stories. The broken canopy was generally 20–25 m high with a few emergents reaching 35 m.

The primary observation lek was comprised of 10 territories (Fig. 1). This particular lek was monitored almost daily from ground level blinds 10-25 m from the main display perches. Initially, observations were concentrated at the seven clustered territories; however, one of them was destroyed by a felled tree in late August.

The boundaries (length by width) of each territory were determined by mapping territorial conflicts and the daily movements of the resident male throughout the study. Height of the main perches were rounded to the nearest 0.5 m (Table 1). Dimensions of the display areas were rounded to the nearest 1.0 m. The "main perch to main perch" measurement is the distance from the main perch in a particular territory to the main perch of the nearest territory. In territory 3 (hereafter T3) the main perch used from September through the termination of the study was measured. The main perches of T6 were destroyed before they could be measured. During the initial 3 weeks of the study, approximately 50 individuals (including all territorial owners) were mist-netted and banded with unique color combinations (celluloid leg bands).

Recordings were made with a Uber 4000 Report L tape recorder and Dan Gibson electronic
Fig. 1. *P. fasciicauila* lek. Study was concentrated at the six territories indicated by the unbroken lines. The owner of territory 6 (dashed line) abandoned it in August after a felled tree destroyed the main perches. Distances from the stream and the three peripheral territories (indicated by X’s) to the clustered territories were estimated.

parabolic microphone (model P500) and were analyzed with a Kay Sonograph Spectrum Analyzer 6061B. Due to the high level of insect noise during many of the recordings, it was necessary to make tracings from the original spectrograms. All spectrograms were made at normal speed and with a wide-band pass filter.
Table 1
Dimensions (M) of six Pipra fasciicauda Territories

<table>
<thead>
<tr>
<th></th>
<th>Height of main perch</th>
<th>Size of display area</th>
<th>Intermale distance*</th>
</tr>
</thead>
<tbody>
<tr>
<td>T1</td>
<td>4.5</td>
<td>20 × 30</td>
<td>29 (T3)</td>
</tr>
<tr>
<td>T2</td>
<td>4.0</td>
<td>18 × 40</td>
<td>14 (T4 &amp; T3)</td>
</tr>
<tr>
<td>T3</td>
<td>3.0</td>
<td>20 × 20</td>
<td>14 (T2)</td>
</tr>
<tr>
<td>T4</td>
<td>4.5</td>
<td>18 × 45</td>
<td>14 (T2)</td>
</tr>
<tr>
<td>T5</td>
<td>5.0</td>
<td>30 × 32</td>
<td>37 (T3)</td>
</tr>
<tr>
<td>T7</td>
<td>5.0</td>
<td>20 × 25</td>
<td>45 (T1)</td>
</tr>
</tbody>
</table>

* Distance of main perch to nearest neighbor’s main perch.

Dimensions of the Display Area

The various parameters of the territories studied are given in Table 1. Most main perches were nearly horizontal or only slightly inclined. Diameter of main perches varied from ca. 10 mm (T4)–ca. 20 mm (T3). With the exception of T3, height of the main perch was similar between territories. Territory 3, the most centrally located, had the smallest display area.

Age and Sex Differences in Coloration

As in most lekking species of manakins, P. fasciicauda shows strong sexual dimorphism in plumage. The colorful adult males are clad with striking red, orange, yellow, white, and black feathers (see Frontispiece). The irides are always white. Snow (1962a, b) showed that immature males of White-bearded (Manacus manacus) and Golden-headed (P. erythrocephala) manakins acquire adult plumage at the beginning of their second year of life, and Foster (1977, 1981) determined that male Swallow-tailed Manakins (Chiroxipha caudata) do not obtain adult dress until the second or third year, while male Long-tailed Manakins (C. linearis) require from 2–4 years. In P. fasciicauda first-year males seem indistinguishable morphologically from females. The upper parts of immature males and females are uniform olive-green. The breast is yellowish olive-green with the belly and undertail coverts a washed-out yellow. It appears that immature males acquire some adult plumage characters (various amounts of red, yellow, and black) after the first post-juvenal molt. Many females exhibit varying degrees of male plumage characters (Graves 1981). The irides of young males and females vary from brown to gray. Immature males gradually acquire the all white iris. However, irides of adult (skull pneumatized)
Fig. 2. Tracings of sound spectrograms of vocalizations of P. fasciicauda. All tracings were made from original spectrograms and represent the typical pattern of each vocalization. Shown above are the advertisement call (A), two adult males giving the advertisement call in unison (simultaneous call) (B), the “normal” (C), partial (D), and the slurred (E) display calls, two examples of the appeasement whistle given in sequence by the same individual (F), and the culminating call (G). (See text for explanation and function of each vocalization.)

females vary from gray to magenta to white. The legs of all birds are pinkish-purple.

Female-plumaged birds that neither called nor displayed during prolonged visits were assumed to be females. All birds that exhibited some display were considered to be males.

SUMMARY OF SOCIAL ORGANIZATION

A typical Band-tailed Manakin lek consists of several males that maintain closely packed territories. Associated with each court or territory within the lek is an alpha, usually a beta, and occasionally one or more nonterritorial (visitors) adult males that perform coordinated displays to attract and excite females. Alpha males are extremely sedentary and dominate all interactions within their respective territories. Beta males are less sedentary and may display with more than one alpha male per day. Beta
males inherit ownership of territories. Nonterritorial males usually display only briefly at any particular territory and are subordinate to both alpha and beta males. Once a female arrives at a territory, it is only the alpha male that actively courts her. A detailed account of the social organization will be presented in another paper (Robbins, unpubl.).

VOCALIZATIONS AND DISPLAYS

To facilitate comparisons, I have adopted the terminology of Schwartz and Snow (1978) to describe the calls and displays of Pipra fasciicauda that are clearly homologous with those of P. filicauda.

Vocalizations

“ Advertisement call.”—This is the most frequently heard call at P. fasciicauda leks. It is the homologue of the “call” of P. filicauda described by Schwartz and Snow (1978). This vocalization, eeeew, is downwardly inflected, from about 5.0–2.5 kHz, and is about 0.5 sec long (Fig. 2A). This call is fairly loud and can be heard more than 100 m away. The caller is always perched; the bill is usually closed and raised 45–60°. The throat is slightly puffed, and the tail is spread, exposing the yellow-white tail band.

While this call undoubtedly advertises a male’s location, this function is likely of limited significance since most adults are probably familiar with the location of the lek. The primary function appears to be to signal that an individual is on his court. A territorial owner invariably calls whenever another manakin passes through his display area. Often the owner gives the call immediately after moving from one perch to another.

An adult male visitor usually gives the call upon entering a resident male’s territory. Frequently an owner and a visiting adult will give the call almost simultaneously (Fig. 2B). Either bird may initiate the call. If the birds are in close proximity, they will raise their bills in unison and call.

“ Appeasement whistle.”—This vocalization is a soft, whistled, single note sweee, gradually inflected upward from about 2.3 to 4.4 kHz (Fig. 2F). Almost invariably (one exception), the caller is motionless in a normal perched position. The bill may be slightly opened when the call is delivered. Duration is variable, about 0.4 to 0.6 sec or longer, with the same individual occasionally intermingling short and long whistles.

This whistle appears to convey a passive or nonaggressive state of the caller. Commonly, the alpha male, often with feathers puffed out, gives this call early in the morning before display is initiated. Presumably, this signals that a bird is not motivated to display. Likewise, at other times the whistle is given by a visiting bird, apparently to signal that it is not inclined to display with the alpha male. The visiting bird will continue
giving the whistle even after the territorial owner has failed to entice it to
the main perch with displays. In addition, the vocalization seems to be
used to indicate that the caller is not aggressively inclined. For instance,
after a chase sequence one or more of the participants will sit on different
perches and give the call.

"Display call."—This abrupt call seems to be given to encourage a bird
to display. It is given only from a perched position. The bill is pointed
upward about 25–45° and is slightly opened, and the throat is slightly
puffed as the vocalization is delivered. The tail is closed. There are three
well-defined variations of this call. The "normal" type is composed of three
elements, a somewhat harsh we-ee-eeh (Fig. 2C). It is given by the alpha
male when a visiting bird delays in coming to the main perch to display.
Once a display bout has begun, the alpha male virtually never gives the
display call. However, a visiting adult male may give this call in the in-
terval between the time the alpha male leaves the main perch and his
return with a "swoop-in flight." BA beta male of T1, gave this call about
35% (N = 394 flights) of the time during swoop-in flights by the alpha
male. When exchanges between the alpha and beta males are rapid and
smoothly coordinated, the vocalization is given less frequently. For ex-
ample, it was given by the beta male (BG of T5) on only 3 of 23 swoop-in
flights performed by the alpha male (RW) during one rapid and well-co-
ordinated display bout (40 swoop-in flights in 14 min). After a break in
display, while both birds are resting, the alpha male may give the display
call to initiate another round of display.

One distinct variation, referred to as the "partial display call," consists
of only the first part of the "normal" call, a weee, about 0.25 sec long (Fig.
2D). It is given by an alpha male when a visiting bird (adult male- or
female-plumaged) fails to join in display. On these occasions, the owner
will fly to the same perch or one adjacent to the uncooperative bird and
give the call until the visitor either joins him in display or leaves the
territory. In one extreme case, the alpha male, BKR of T2, gave more
than 25 of these calls before the visitor left the display area. This version
may also be given by either bird of a displaying duet, while on the main
perch, when the returning partner (during a swoop-in flight) flies over the
perch instead of landing on it. In addition, this call is given more often
when two or more males are competing for dominance (particularly during
July and August in T2 and T3). A perched male may give the "normal"
display call while two or more birds chase each other around the display
area. If the chasing continues without any bird joining him in display, he
often gives the partial display call. If the chase still continues, he may
pursue one or more of the other males.

The third pattern, referred to as the "slurred display call," has an ad-
ditional note that follows about 0.5 sec after the normal version (Fig. 2E). The fourth note is lower in frequency and nearly as long in duration as the "normal" pattern. This call is usually given by the territorial owner when no other birds are present in the display area. This is particularly true in the early morning before any other bird has arrived and late in the afternoon when most display has subsided. The function of this call appears to be the same as that of the above two versions, i.e., to attract other birds to display. The addition of another note of lower frequency probably enhances the transmission of this call over greater distances. Morton (1975) and Marten et al. (1977) have demonstrated that rain forest sounds of lower frequency carry farther than sounds delivered from the same height at a higher frequency.

"Culminating call."—This vocalization (Fig. 2G), a prolonged eeeooo, is given only during a swoop-in flight. A male performing the swoop-in flight delivers the call the instant before he reaches the main perch. It is rarely omitted during solo performances or between well-acquainted male partners. Between displaying twosomes, the call is usually omitted only when the passive bird fails to bend forward and fly to an adjacent limb as the active male swoops up to the perch. In these instances, the active bird may either land quietly next to the passive bird or will swoop over his head to an auxiliary perch. Immature males rarely give the call. This vocalization may serve in accenting the termination of a swoop-in flight.

"Klok."—This low intensity call is apparently mechanically produced (probably by the wings). Schwartz and Snow’s (1978) phonetic representation (klok) of the homolog of this call in P. filicauda, accurately describes the sound produced by P. fasciicauda. The klok (Fig. 3A) consists of two pulses of sound about 0.005 sec apart. It is produced primarily in the instant before or upon landing on a perch. Likewise, during a swoop-in flight, a klok is produced as a male lands at the distant perch before he returns to the main perch. This sound appears to accent the arrival of a male at a perch.

"Kloop."—Like the shorter klok, this low frequency call is apparently produced by the wings (Fig. 3B). It is produced at the lowest point of a swoop-in flight the instant before the male quickly ascends to the main perch. As with the klok, the kloop probably increases the conspicuousness of the male to other birds. The kloop and the culminating call indicate that a swoop-in flight has just been performed.

DISPLAYS

"Side-to-side display."—An individual performing this display is oriented perpendicular to the perch. The body is held rigid, slightly tilted upward, while the head is raised about 45–70°. The crown and upper
mantle feathers are depressed. Normally the bird performs several rapid, short (1–2 cm) hops to one side then back to the original position. The displaying bird usually hops no more than 10 cm in either direction. During this display the bird has a preferred direction that he faces. For example, the direction of orientation was nonrandom for all four alpha males analyzed (Fig. 4). Rarely (<4%, N = 339 observations), a bird may perform
Lig. 4. Degree of asymmetry of two different orientations of the side-to-side display. Solid arrows exhibit the degree of asymmetry (in %) of the direction an alpha male faces while performing the display. This orientation was nonrandom for all alpha males (binomial test, \( P < 0.05 \), Conover 1971). Cross hatched arrows represent (in %) the degree of asymmetry in the subsequent direction of hopping. Only alpha male, BW, hopped in a nonrandom direction (\( P < 0.05 \)). Data were too few to analyze the degree of asymmetry in the direction of hops of RB.

In one direction, stop, turn around, and display facing in the opposite direction. An owner may have a preferred direction, right or left, to which he hops during each series, although some individuals exhibit no preference, e.g., two of the three alpha males analyzed hopped randomly (Fig. 4). On rare occasions (<3%, \( N = 494 \) observations), when a bird is especially excited, it may hop in one direction, return to the original position, and then hop in the opposite direction. I do not know whether preferences are reflections of innate “right-or-left-handedness” or of orientation toward some unknown feature of the display site environment.

The territorial owner is the principal performer of this display, e.g., Bl-R 97% (\( N = 207 \)), BW 95% (\( N = 168 \)), RB 93% (\( N = 29 \)), and RW 75% (\( N = 142 \)), although a beta male and/or a nonterritorial male will occasionally perform the display. Most displays are conducted on the main
perch, e.g., B1-R 86% (N = 207), BW 90% (N = 168), RB 100% (N = 29), and RW 68% (N = 142). Displays not performed on the main perch are invariably performed on nearby auxiliary perches. The side-to-side display invites a visiting bird to join the performer on the main perch. Its duration is dependent on the response of the visiting bird. If a visitor immediately moves to the main perch, the performer may terminate the display after a single series of hops. However, if the visitor delays, the displayer may perform several series. On two occasions, B1-R (alpha male of T1) performed this behavior for over 2 min with only a few brief (1–4 sec) pauses.

"Short flight."—This is a common element of the display repertoire of *P. fasciicauda*. It may precede or follow any other display. A resident male usually performs this display immediately upon detecting the arrival of another bird in the display area. He usually flies with a normal flight pattern from one perch to another, in a more or less horizontal plane, and the instant before or upon landing produces a *klok*. Not uncommonly, the resident male performs several of these in rapid succession between two perches, primarily the main perch and an adjacent perch. This not only enhances the conspicuousness of the male, but may aid in drawing the visitor's attention to the main perch.

"Stationary display."—The head is tilted forward, and the body is held nearly horizontal, while the wings are lowered slightly and quivered. The crown and nape feathers are depressed. The lower back feathers may be slightly erected. This behavior may precede or follow any other display and may be performed on any display perch. This display is exhibited when a male is anticipating the actions of another bird. This display was most frequently given when three or more birds were present in a territory. Often one of the birds, observing from a perch, would exhibit stationary displays when two other birds were chasing one another around the display area.

"Horizontal freeze."—The posture of a male performing this display is reminiscent of the stationary display except in the freeze the body, wings, and tail are held in a rigid horizontal position, with the crown and upper mantle feathers depressed. The pupils are contracted. Unlike the stationary display, however, this display is only exhibited in the presence of a female-plumaged bird. On four occasions this behavior was observed without any apparent female-plumaged birds present; however, the male may have detected a female I did not notice. A swoop-in flight followed by a short flight to an adjacent perch immediately precedes the majority of the freezes. This may be one of the ways males assess the receptiveness of females during the course of courtship. Movement by a female during the display appears to initiate an immediate response by the male. For ex-
ample, if the female returns to the main perch the male immediately terminates the freeze and will initiate another form of display. The duration of this display appears to be dependent on the female’s actions. Males may remain in this frozen posture up to 10 sec, although the freeze usually lasts no more than 5 sec.

"Butterfly display."—This conspicuous display is performed by an adult male that flies in a more or less direct horizontal plane between display perches (Fig. 5). The flight is deliberate with shallow wing beats. The wings appear to be held fairly stiff and are extended to maximally exhibit the white of the primaries and secondaries. No calls are given during the display, although occasionally a bird will produce a klok upon landing. It
may precede or follow any other display and is never performed in the absence of another bird.

"Aerial chase."—This rarely-occurring display (N = 20) was observed only during July and August in territories 2 and 3. The display is similar to the butterfly display: participants fly with slow, shallow wing beats conspicuously displaying the white areas of the flight feathers. In contrast to the butterfly display, two birds are always involved, with one chasing the other around in a series of wide loops through and above the display area. The rate of flight is more rapid than a butterfly display. Some of these chases lasted over a minute without either bird landing; one chase lasted about 3.5 min with a 20-sec pause when both birds rested on perches. In all cases, the aerial chase was observed in the presence of three or more adult-plumaged males in the display area. At least three chases terminated in flights. In territory 3, every instance (N = 7) involved a visitor, BY or RG, chasing another visitor, BB. The alpha male BWB never participated. Unfortunately, the identity of both participants was not determined in most chases in T2. This display may be one of the means by which a visiting male establishes dominance over other visiting males. Only once was a vocalization heard during the display; in this single instance, one of the participants gave a quivering appeasement whistle.

"Flutter."—This is the copulatory position of a male. The male appears to be falling backward off a perch, with wings spread and rapidly beating, while the head and upper body are slightly tilted forward. At times a male may perform the flutter while raised on his toes. Most instances of this behavior were not during actual copulation but during pseudo-copulations with branches. In these instances, a male flies to a perch and performs the flutter, making contact between the cloacal region and the perch. Most of these pseudo-copulations lasted no more than 4 sec. In 50% of the cases (N = 110), the flutter followed a swoop-in flight. On six occasions immature males were observed performing this act. Whether this is an innate response to rising hormone levels or an imitation of other performing males is not clear.

"Tail-up freeze."—Once a male has attracted another bird, male or female, to his display perch, he may perform a tail-up freeze (Fig. 6). The male orients the cloacal region to the visiting bird. The head is tilted downward 15–25°, and the tail is erected to a 60–80° angle. The black lower back feathers and upper tail coverts are erected. The wings are drooped somewhat and vibrated very rapidly, exposing a small patch of white in the underside of the wings. This appears as a white blur bordered by the black of the rest of the wing. The crown and upper back feathers are depressed, while the pupils are contracted. A male performing this display usually remains stationary; however, when a displaying bird be-
comes extremely excited, he may twist from side-to-side. The performer’s feet appear to remain stationary during the twisting. Very rarely, a male may back toward the visitor while performing this display.

A visiting bird is confronted with a conspicuous area of yellow as it faces the posterior of the displaying bird. This area is bordered by the black of the tail, and the vent region is accented by the black and white blur of the vibrating wings. Usually this display lasts 3–4 sec before the displaying bird initiates a swoop-in flight; however, the duration varies depending on the response of the visiting bird.

“Swoop-in flight.”—The swoop-in flight is initiated primarily from the main perch. In most cases, another bird is present, e.g., B1-R (alpha male of T1) performed 94% of his flights (N = 835) in the presence of another bird. During a solo display, the owner leaves the main perch and flies directly to a perch 15–30 m away. This distant perch is always higher than the main perch, e.g., in T1 it was 3 m higher. Upon landing at the far perch, he usually produces a *klok*; he then immediately turns around and quickly swoops downward, producing a *kloop* at the lowest point of the swoop before swinging upward to the main perch. In solo display the culminating call is invariably given the instant before reaching the main perch. As he reaches the main perch, the male quickly turns around (difficult to detect) in mid-air and lands on the perch facing in the direction from which he came. Duration of the display varies according to distance of the far perch. The flights of territorial owner 1 (B1-R) all fell within a 7–8 sec range, whereas those of territorial owner 2 (BKR) lasted 6.5–7.3 sec. Most variation in duration within a single owner’s flights occurs from
the time he leaves the main perch and lands at the far perch; there is virtually no variation in the return part of the display.

"Joint display between males."—Most displays between males involve a territorial owner and another adult-plumaged male usually familiar with the owner and his display area. Once the owner has detected another male, he may perform a few short flights and give an advertisement call or two, or rarely a butterfly display before he moves to the main perch and does a side-to-side display. After the visiting bird has been enticed to the perch, the owner may perform a tail-up freeze, but more frequently, especially among "well-acquainted" partners, i.e., alpha and beta males that have displayed together for at least several days, he will immediately initiate a swoop-in flight. This type of swoop-in flight is identical to that conducted in the absence of another bird, except that the visiting male often may give a normal display call in the interval between departure of the territorial male from the main perch and his return. Only the visiting male gives the normal display call during display bouts. The instant before a returning male gives the culminating call and lands, the passive bird may give an advertisement call just before the active male delivers the culminating call (Fig. 3b). The passive male then flies to the far perch and performs a swoop-in flight, exchanging positions with the other bird on the main perch. In well-acquainted pairs, the passive bird often will fly directly to the far perch following an exchange, and will rapidly return with a swoop-in flight. These highly-synchronized displays are very impressive and may continue for several minutes. When a pair resumes displaying after a short break, it is usually the alpha male that initiates the bout. Displays between owner and visiting adult male are not necessarily well coordinated, particularly if the visiting bird is very aggressive. In uncoordinated display the visitor may fail to bend down and fly off as the owner approaches the perch during a swoop-in flight or the visitor may fail to conduct a swoop-in flight after the alpha male has done so. In these instances, the owner will either swoop over the main perch or, less frequently, will land next to the uncooperative bird. Displays involving the owner and immature males are usually short and uncoordinated.

"Male and female interactions."—In contrast to male-male interactions, presumed females do not join in displays and apparently almost never call while on the lek. As mentioned earlier, this behavior was used to distinguish females from immature males, as females often exhibit some male plumage characters (Graves 1981). During brief visits by female-plumaged birds, it was often impossible to determine their sex.

As with male-male interactions, the alpha male may perform several short flights, occasionally a butterfly display, and give an advertisement call or two before moving to the main perch to perform a side-to-side invitation.
After the female has been enticed to the display perch, the male usually performs the tail-up freeze. If the female should move to an adjacent perch, the male may give an advertisement call and then perform another series of side-to-side displays until the female rejoins him. He may again perform a tail-up freeze before rapidly flying from the perch to perform a swoop-in flight. In 92% (N = 59) of the swoop-in flights the female bent down and flew to an adjacent perch just as the male reached the main perch. The male will often perform a horizontal freeze immediately following a swoop-in flight, or he may perform a short flight from the main perch to a nearby perch before exhibiting the horizontal freeze. After this he may perform a butterfly display or one or two short flights. If the female has not returned to the main perch, he will move there and perform another side-to-side display. I never saw an owner pursue a female once she left his area. Usually a male performed a few short flights, or, if his regular partner was present, they would perform a series of swoop-in flights in an apparent attempt to attract the female back to the area.

In the only copulation observed, the alpha male (BKR) and the beta male (WB) performed several swoop-in flights before I detected the female. The beta male did a short flight followed by a horizontal freeze (ca. 10 sec long). The alpha male flew to the main perch while the beta male performed a few more short flights. The alpha male then did a side-to-side display. As soon as the female moved to the main perch, the alpha male immediately initiated a swoop-in flight. Upon returning he did the usual turn-around in mid-air, but instead of landing on the perch, he landed on the female’s back and copulated with her for ca. 2.5 sec. During the copulation, the female was bent forward slightly (about 30°). The male rapidly flapped his wings as in a flutter display. After completion, the female flew to an adjacent perch before flying from view. The beta male joined the alpha male, and both gave a few advertisement calls.

Table 2 summarizes the conditions when calls and displays are given by alpha male P. fasciicauda.

## COMPARISON WITHIN THE SUPERSPECIES COMPLEX

Making behavioral and ecological comparisons between closely related species pinpoints the differences that have arisen since speciation of a particular group. Such a comparison not only may reveal evolutionary pathways within a particular group, but also may elucidate general patterns of evolution of behavior.

A detailed comparison of displays can now be made between P. fasciicauda and P. filicauda, within the superspecies complex. Observations for P. aureola are still incomplete. Nevertheless, some notable trends can be discerned among the three species (Table 3).
Table 2
Situations in which Alpha Male Pipra fasciicauda Call and Display

<table>
<thead>
<tr>
<th>No other bird present</th>
<th>Another male present</th>
<th>Female present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Advertisement call</td>
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<td>X</td>
</tr>
<tr>
<td>Simultaneous call</td>
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<td>X</td>
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<tr>
<td>Appeasement call</td>
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<td>X</td>
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<tr>
<td>Display call</td>
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<tr>
<td>Normal</td>
<td>—</td>
<td>X</td>
</tr>
<tr>
<td>Partial</td>
<td>—</td>
<td>X</td>
</tr>
<tr>
<td>Slurred</td>
<td>X</td>
<td>—</td>
</tr>
<tr>
<td>Culminating call</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Klok</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Kloop</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Side-to-side display</td>
<td>—</td>
<td>X</td>
</tr>
<tr>
<td>Short flight</td>
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<td>X</td>
</tr>
<tr>
<td>Stationary display</td>
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<td>X</td>
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<tr>
<td>Horizontal freeze</td>
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<tr>
<td>Tail-up freeze</td>
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<td>X</td>
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<tr>
<td>Swoop-in flight</td>
<td>X</td>
<td>X</td>
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</tbody>
</table>

* The simultaneous call, appeasement whistle and normal display call are rarely given when a female is present.
* In most instances, the aerial chase involves the beta and a nonterritorial male.

Vocalizations and displays are remarkably similar between P. filicauda and P. fasciicauda. Presumably, these strong similarities are shared by P. aureola, as P. fasciicauda and P. aureola are more similar morphologically than either is to P. filicauda. All three species exhibit the side-to-side display, short flight, and swoop-in flight apparently common in one form or another to all Pipra studied so far (Snow 1963b, Sick 1967). The orientation of a male’s posterior region toward a visitor is also widespread in Pipra. Every species in the Red-capped Manakin (P. mentalis) complex ([P. mentalis], [P. erythrocephala], Red-headed [P. rubrocicilla] and Round-tailed [P. chloromeros] manakins) has a black posterior that is highlighted by either bright yellow or red feathered thighs. This orientation may have led to the evolution of striking plumage patterns in the posterior region of Blue-rumped (P. isidorei), Cerulean-rumped (P. caeruleocicilla), White-fronted (P. serena), and Snow-capped (P. natterei) manakins, though little is known about the display of these species. Within the P. aureola complex, the differences in visual (and tactile in P. filicauda)
Table 3
Comparison of Display Within the Superspecies Complex

<table>
<thead>
<tr>
<th></th>
<th>P. aureola</th>
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<th>P. filicauda</th>
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<td>+</td>
<td>+</td>
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<tr>
<td>Appeasement whistle</td>
<td>?</td>
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<td>and appeasement patterns</td>
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<td>Display call</td>
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<td>Slurred</td>
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<td>Culminating call</td>
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<td>Klok</td>
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<td>Side-to-side display</td>
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<td>Short flight</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Stationary display</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Horizontal freeze</td>
<td>?</td>
<td>+</td>
<td>?</td>
</tr>
<tr>
<td>Butterfly display</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Flutter</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Aerial chase</td>
<td>?</td>
<td>+</td>
<td>?</td>
</tr>
<tr>
<td>Tail-up freeze</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Twist</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Swoop-in flight</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Coordinated display</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>between males</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* +, − or ? indicates the presence, absence or uncertainty of a behavior in the species repertoire.

stimulation exhibited to a visitor during the tail-up freeze may be important isolating mechanisms. The vent region of male *P. aureola* and *P. filicauda* is primarily black, although the bright breast feathers (red in *P. aureola*, yellow in *P. filicauda*) extend narrowly into this region. In contrast, the vent area of *P. fasciicauda* is almost entirely yellow.

Unlike all other *Pipra*, *P. fasciicauda* and *P. filicauda* have unique tail patterns. The yellowish-white tail band of *P. fasciicauda* is most conspicuous when the bird gives the advertisement call. The coevolution of the elongated tail filaments and the "twist" in *P. filicauda* has resulted in one of the most unusual behaviors in the family (Schwartz and Snow 1978). Several piprids have lengthened tail feathers; however, only *P. filicauda* is known to use the modified feathers for tactile stimulation. Schwartz and Snow (1978) suggested that the twist of *P. filicauda* possibly evolved from an about-face movement, i.e., pivoting. The about-face movement is unreported for *P. aureola*. *P. fasciicauda* exhibits some pivoting (the feet do not appear to move) during the tail-up freeze. Since all three species ex-
hibit the tail-up freeze, it seems likely that the twist of *P. filicauda* may have been derived from it. Upon isolation, selection may have favored male *P. filicauda* that adopted movement during the tail-up freeze. Occasional contact between the male’s tail and the female during this display may have promoted the coevolution of the long tail filaments and the twisting motion in *P. filicauda* (Schwartz and Snow 1978). Females of *P. fasciicauda* occasionally hop quite close to a male performing the tail-up freeze, almost making contact with his tail and vent region. On four occasions, immature males of *P. fasciicauda* pecked at the erected lower back feathers, tail and/or undertail coverts of an adult male during this display. Schwartz and Snow (1978) noted this same phenomenon exhibited by immature males of *P. filicauda* during the twist.

Another notable plumage characteristic restricted to the *P. aureola* complex is the presence of white in the flight feathers. This striking feature further enhances the conspicuousness of the displaying males. It is evident in all flight displays and aids in accenting the vent region during the tail-up freeze. Furthermore, the degree of coordination between displaying males of this complex is apparently unequaled by other *Pipra* and surpassed in Pipridae only by *Chiroxiphia spp*. The aerial chase is unreported for *P. filicauda* and *P. aureola*; however, this relatively rare behavior may go undetected without prolonged study. The aerial chase and the butterfly display are very similar behaviors, with both incorporating the relatively slow, conspicuous wing beat. The precursor of these displays may have developed out of conflicts between two (or more) birds when one individual chased another around or from his territory. Competing males may have adopted the slower wing beat as a means of reducing the intensity of chases. Presumably, males were gradually acquiring more conspicuous plumage, e.g., increased white in the wings. With the gradual decrease in aggression between males, allowing for the evolution of joint display, the chase behavior may have been incorporated into the nonaggressive, highly-ritualized butterfly display, with its subsequent decrease in use in conflicts. This may explain why the aerial chase is relatively rare and occurs only when there is intense competition for a territory between three or more males.

As with the aerial chase, the lack of observation of the horizontal freeze in the other two species may be an artefact of short term studies. This display may have evolved from the more generalized stationary displays, since in both displays the bird is horizontal (more so in the freeze) and anticipates the action of another bird (only females in the freeze).

The swoop-in flights of *P. filicauda* and *P. fasciicauda* differ in two notable ways. Whether in solo or joint display, male *P. fasciicauda* terminate the swoop-in flight on the main perch. The only exception is during
duets when the passive partner fails to bend down and fly as the active bird approaches the perch. In such instances, the active male will either fly over the main perch or, less frequently, will land quietly next to the passive bird. This contrasts sharply with similar behavior of *P. filicauda*, wherein usually, either in solo or duets, the performer over flies the main perch and lands on a nearby one (Schwartz and Snow 1978). In addition, male *P. fasciicauda* give only a single culminating call at the termination of a swoop-in flight. Schwartz and Snow (1978) identified two different, but quite similar, calls in *P. filicauda* that are given under different circumstances at the termination of the swoop-in flight. The first, and most frequently given, the pass-by call, is delivered by an active bird as it flies over the main perch and lands on an auxiliary perch. The second, somewhat longer version, is given when the male flies over and then veers back to the main perch.

Schwartz and Snow (1978) distinguished two types of soft, *sweee*, whistles of *P. filicauda*. Shorter whistles (<0.4 sec) were termed “conflict whistles,” while longer ones (>0.5 sec) were referred to as “appeasement whistles.” I recorded both short and long as well as intermediate whistles for *P. fasciicauda* that are similar to those of *P. filicauda*. The whistle is more gradually inflected upward in *P. fasciicauda*. In *P. fasciicauda* there seemed to be little distinction in context between short and long whistles, since the same individual may intermix them.

The duration of the advertisement call of *P. fasciicauda* is almost twice that of *P. filicauda*. The “normal” and partial display calls are apparently nonexistent in *P. filicauda*. However, a spectrogram in Schwartz and Snow’s (1978: Fig. 3K) paper is similar to that of the slurred display call of *P. fasciicauda*. Schwartz and Snow (1978) did not determine the function of the call represented in the above spectrogram; however, since the call is apparently given under similar circumstances to that of *P. fasciicauda*’s slurred display call, it probably serves the same function, i.e., to attract birds to display. One of the calls, a double-noted *chee-weep*, described by Snow (1963A) for *P. aureola* may be a homologue of the “normal” display call of *P. fasciicauda*.

The display sites of *P. fasciicauda* and *P. filicauda* apparently differ notably. However, caution must be exercised in comparing display sites until each species has been studied under a variety of situations. The understory in *P. filicauda* leks is apparently more open than that in *P. fasciicauda* leks; in fact, Schwartz and Snow (1978:55) mention that the understory below 2–4 m at *P. filicauda* leks is particularly bare, with only “a sparse to moderately dense scattering of sapplings and vines.” All display sites of *P. fasciicauda* (five different leks were visited) had dense vegetation below 2 m. Foliage density above 2 m varied from moderate to
heavy. These differences in vegetation structure may explain why the main
perches of \textit{P. fasciicauda} are consistently higher than those of \textit{P. filicauda}.
Schwartz and Snow (1978) found no \textit{P. filicauda} territories to be contiguous;
in contrast, several \textit{P. fasciicauda} territories were contiguous. Comparison of other behavioral and ecological aspects must await more
detailed studies of \textit{P. aureola} and \textit{P. filicauda}.

In summary, the above comparisons, particularly between \textit{P. filicauda}
and \textit{P. fasciicauda}, further support the suggestion of Haffer (1970) and
Schwartz and Snow (1978) that \textit{P. aureola}, \textit{P. fasciicauda}, and \textit{P. filicauda}
comprise a superspecies.

\section*{SUMMARY}

Color-marked Band-tailed Manakins (\textit{Pipra fasciicauda}) were studied for 6.5 months in
undisturbed lowland rain forest of southeastern Peru in 1980. Males congregate at localized,
naturally disturbed areas in seasonally flooded forest. The display of \textit{P. fasciicauda} differs
from most other manakins in that usually two or more males perform coordinated displays
to attract and excite females. At each display site, an alpha male (the dominant bird) usually
performs coordinated displays with a subordinate male. Once a female arrives, it is only the
alpha male that actively courts her.

A male's display repertoire consists of several elaborate displays that combine visual and
acoustical elements to enhance his conspicuousness to a female. The acoustical element is
composed of both mechanically and vocally produced sound.

The display repertoire of \textit{P. fasciicauda} is remarkably similar to that of \textit{P. aureola}
and \textit{P. filicauda}. This, combined with the similarity in plumage shared by these species, supports
the contention that the three species comprise a superspecies.

\section*{ACKNOWLEDGMENTS}

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and institutions.

\section*{LITERATURE CITED}


COLOR PLATE

The colorplate Frontispiece of the Band-tailed Manakin (Pipra fasciicauda) has been made possible by an endowment established by the late George Miksch Sutton. Painting by F. P. Bennett, Jr.
SEASONAL VARIATION IN MOBBING INTENSITY IN THE BLACK-CAPPED CHICKADEE

DOUGLAS H. SHEDD

Several studies have indicated that mobbing behavior in some species of birds is most intense during the breeding season (Altmann 1956, Horn 1968, Root 1969, Curio 1975, Shedd 1982). In Shedd (1982), I suggested that in some migratory species, such as the American Robin (Turdus migratorius), one might expect mobbing to be absent or less intense outside the breeding season, because at this time birds are not confined to territories, and because they are not defending young. Many species of birds, however, do mob predators outside the breeding season. Here I present information for such a species, the Black-capped Chickadee (Parus atricapillus).

METHODS

From 1 June 1974-31 August 1976, field trials were performed on a weekly basis in the vicinity of Ithaca, Tompkins Co., New York. The procedure during these trials simulated a natural mobbing episode. A mounted Eastern Screech-Owl (Otus asio) was placed in a conspicuous location 2 m from the ground. A recorded screech-owl call was then played from a speaker located 10 cm from the mounted specimen. All trials were observed from concealed positions 10 m from the mount. To reduce the likelihood of habituation, care was taken not to perform a trial at a study site more frequently than once every 5-7 days. The total number of trials in each month varied; in general, there were fewer total trials during the winter months because bad weather limited access to study sites (Table 1).

Data from the study period were totaled and then treated as a single 12-month series. For each month, the average number of minutes of mobbing per bird (AMM/B) was calculated by summing minutes of mobbing and dividing by the total number of mobbing birds. The percentage of successful trials (trials that resulted in mobbing) and the average number of mobbing birds per successful trial were also calculated for each month.

The equality of monthly means was tested using a single classification ANOVA, with means weighted according to the reciprocal of the variance of the samples from which they were drawn. This adjustment results in an approximate test of equality of means when variances are heterogeneous (Snedecor 1956, Sokal and Rohl 1969). Further details concerning methods and study areas may be found in Shedd (1982).

RESULTS

Chickadees were abundant during all months of the year in Ithaca and were observed mobbing the mounted owl in each month of the study. The AMM/B index ranged from a maximum of 4.2 min of mobbing/bird in August to a minimum of 1.8 min of mobbing/bird in January ($P < 0.05$, $F = 2.448$). In general, AMM/B values were high from July through September, and then somewhat lower at other times of the year (Table 1).
Table 1
Percentage of Successful Trials, Average Minutes of Mobbing/Bird (AMM/B), and Average Number of Birds/Successful Trial for Each Month (Ithaca, New York)

<table>
<thead>
<tr>
<th>Month</th>
<th>Total trials</th>
<th>Successful trials</th>
<th>Total birds</th>
<th>Percentage of successful trials</th>
<th>AMM/B</th>
<th>Average number of birds/successful trial</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>35</td>
<td>19</td>
<td>67</td>
<td>57.1</td>
<td>1.8</td>
<td>3.5</td>
</tr>
<tr>
<td>February</td>
<td>18</td>
<td>5</td>
<td>20</td>
<td>27.8</td>
<td>2.2</td>
<td>4.0</td>
</tr>
<tr>
<td>March</td>
<td>37</td>
<td>18</td>
<td>57</td>
<td>48.7</td>
<td>2.9</td>
<td>3.2</td>
</tr>
<tr>
<td>April</td>
<td>59</td>
<td>26</td>
<td>79</td>
<td>44.1</td>
<td>2.9</td>
<td>2.9</td>
</tr>
<tr>
<td>May</td>
<td>103</td>
<td>39</td>
<td>63</td>
<td>37.9</td>
<td>2.5</td>
<td>1.7</td>
</tr>
<tr>
<td>June</td>
<td>134</td>
<td>59</td>
<td>118</td>
<td>44.0</td>
<td>2.8</td>
<td>2.1</td>
</tr>
<tr>
<td>July</td>
<td>151</td>
<td>64</td>
<td>222</td>
<td>42.0</td>
<td>4.1</td>
<td>3.5</td>
</tr>
<tr>
<td>August</td>
<td>172</td>
<td>77</td>
<td>284</td>
<td>44.8</td>
<td>4.2</td>
<td>3.7</td>
</tr>
<tr>
<td>September</td>
<td>91</td>
<td>54</td>
<td>215</td>
<td>59.3</td>
<td>3.7</td>
<td>4.0</td>
</tr>
<tr>
<td>October</td>
<td>95</td>
<td>49</td>
<td>172</td>
<td>51.6</td>
<td>2.5</td>
<td>3.6</td>
</tr>
<tr>
<td>November</td>
<td>54</td>
<td>19</td>
<td>73</td>
<td>35.2</td>
<td>2.3</td>
<td>3.8</td>
</tr>
<tr>
<td>December</td>
<td>29</td>
<td>13</td>
<td>62</td>
<td>44.8</td>
<td>2.0</td>
<td>4.8</td>
</tr>
</tbody>
</table>

* Average number of minutes of mobbing per bird.

The percentage of trials successful in producing mobbing varied from a high of 59.3% in September to a low of 27.8% in February (Table 1). The percentage of successful trials did not seem to follow any apparent pattern, but rather averaged about 45% of all trials. Values of 50% or higher were recorded in January, September, and October. Values of 40% or lower were recorded in February, May, and November. The average number of birds mobbing during a successful trial varied from a low of 1.7 in May to a high of 4.8 in December ($P < 0.05, F = 6.349$) (Table 1).

In addition to mobbing, chickadees performed three behaviors related to mobbing: silent approach, vocal approach, and attacking (see Shedd 1982). These three behaviors were infrequently observed, however, and no seasonal variation could be detected.

DISCUSSION

The seasonal variation in mobbing intensity displayed by the Black-capped Chickadee is best considered in the context of the annual life cycle of the species. Odum (1941a), working in Rensselerville, Albany Co., New York, found that the first evidence of courtship and pair formation occurred from 10–25 April. Glase (1973), working in Ithaca, New York, found that by the third week in April all dominant males were alone on a territory
with a mate. Glase (1973) gave the mean hatching date in Ithaca as 8 June. Thus, for most of April and May, pairs were on territories, but had no young (note that the average number of birds/successful trial in May was only 1.7). Mobbing intensity during this period was quite low (Table 1).

The relatively low intensity of mobbing at this time may be related to the large size of chickadee territories. In a 2-year study in Utah, Stefanski (1967) found that during the prenesting stage in 1964 territories averaged 1.8 ha, and in 1965 averaged 2.6 ha. Odum (1941a) found that territory size in New York averaged 13.2 acres (5.2 ha). Birds confronted with predators must choose among a variety of predator responses ranging from escape to attack. The balance of risk to gain is the probable factor determining what behavior is displayed. In a situation where pairs without young are living on large territories, it may be that limited mobbing is the most adaptive response to a predator. The fact that females were spending considerable time in incubation during the latter part of May could have also contributed to the low level of mobbing activity in this month.

Odum (1941b) gave a mean fledging date of 23 June and Weise and Meyer (1979) found that families remain together for about 20 days after fledging. Thus, parents could be expected to be on territories with fledged young from late June until mid-July. Odum (1941b) stated that fledging for second broods occurred in late July, so families resulting from second broods would break up in mid- or late August. The AMM/B index peaks during these 2 months (Table 1). This may be the result of the increased vulnerability of the young when they leave a hole-nest at fledging, and of the high parental investment in fledged young (Barash 1975, Gottfried 1979). Also, the post-fledging period would seem to be the time most likely for the cultural transmission of predator recognition and the associated mobbing response if the hypotheses of Curio et al. (1978) and Vieth et al. (1980) are correct. Clearly, the increase in the average number of birds mobbing per successful trial from 2.1 in June to 3.5 in July in part reflects the mobbing performed by recently fledged birds.

Mobbing in chickadees continues after the end of the breeding season. The intensity of mobbing, however, falls from the maximum in July and August to a minimum in December and January (Table 1). This decline in mobbing may be related to the dispersal of young from parental territories to form new flocks. Judging from Weise and Meyer (1979) nonbreeding flocks usually consist of unrelated birds. It may be that intensive post-reproductive mobbing is not adaptive in chickadees, because closely related individuals are not nearby to benefit.

If the above is an accurate assessment of chickadee mobbing, the question remains as to why chickadees continue to mob at all after the breeding season. Some species, such as the American Robin, largely cease mobbing
screech-owls at the end of the breeding season (Shedd 1982). Chickadees differ from robins in at least two ways that may influence mobbing behavior: (1) chickadees (11.2 g) are much smaller than robins (78 g) (Baldwin and Kendeigh 1938); and (2) chickadees are more sedentary than robins.

The small size of adult chickadees in comparison to robins may mean that chickadees are more vulnerable to owl predation than are robins. Thus, chickadees could be expected to respond to owls at all times of the year, while robins respond only during the breeding season, when the more easily captured young are present. The chief argument against this hypothesis comes from a consideration of the diet of the screech-owl, which encompasses species of a variety of sizes, including birds as large as Mourning Doves (Zenaida macroura) (Van Camp and Henny 1975). This hypothesis cannot be dismissed, however, without detailed studies on the fall and winter diet of the screech-owl.

Chickadees and robins both maintain breeding territories. Robins, however, form migratory or nomadic flocks following the breeding season, while chickadees live on winter home ranges in relatively stable flocks consisting of both resident and migrant birds (Odum 1941a, Glase 1973, Mueller 1973, Shedd 1982). Curio (1978) suggested, as part of his "move on" hypothesis of the function of mobbing, Sherman's (1977) idea that more sedentary animals should mob more intensely than less sedentary ones. Living continuously on a territory or home range may mean that mobbing to force a predator away is adaptive at all times of the year, because relocation to avoid further predator encounters is not possible. Thus, for sedentary species, the benefits of causing a predator to "move on" would maintain mobbing at some baseline level that would be increased during the breeding season, as mobbing serves the additional function of protection of the young.

Comparisons of species such as the Black-capped Chickadee and the American Robin indicate the extent to which mobbing can vary from species to species in response to different selection pressures. Mobbing may also vary from individual to individual, and from situation to situation (Shalter 1978). Considerable work remains before a comprehensive explanation of the function and mechanics of this behavior is possible.

SUMMARY

Black-capped Chickadees (Parus atricapillus) were found to mob an Eastern Screech-Owl (Otus asio) at all times of the year. Mobbing was most intense during July and August and least intense during December and January. I suggest that, since chickadees alternate between breeding territories and home ranges, mobbing to force a predator away is adaptive throughout the year. For species that are largely sedentary, the benefits of causing a predator
to move to another location may maintain mobbing at some baseline level that would be increased during the breeding season, as mobbing serves the additional function of protection of the young.

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LITERATURE CITED


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Wilson Society Student Membership Award

THE WILSON ORNITHOLOGICAL SOCIETY is offering an annual membership in the Society to undergraduate and graduate students with a continuing interest in ornithology and who would benefit from their association with our Society. Applications can be obtained from John L. Zimmerman, Div. Biology, Kansas State University, Manhattan, KS 66506. Closing date for receiving completed applications is 15 December 1983.
VEGETATION CHARACTERISTICS IMPORTANT TO COMMON SONGBIRDS IN EAST TEXAS

RICHARD N. CONNER, JAMES G. DICKSON, BRIAN A. LOCKE, AND CHARLES A. SEGELQUIST

Multivariate studies of breeding bird communities have used principal component analysis (PCA) or several-group (three or more groups) discriminant function analysis (DFA) to ordinate bird species on vegetational continua (Cody 1968, James 1971, Whitmore 1975). In community studies, high resolution of habitat requirements for individual species is not always possible with either PCA or several-group DFA. When habitat characteristics of several species are examined with a DFA the resultant axes optimally discriminate among all species simultaneously. Hence, the characteristics assigned to a particular species reflect in part the presence of other species in the analyses. A better resolution of each species' habitat requirements may be obtained from a two-group DFA, wherein habitats selected by a species are discriminated from all other available habitats.

Analyses using two-group DFAs to compare habitat used by a species with habitat unused by the same species have the potential to provide an optimal frame of reference from which to examine habitat variables (Martinka 1972, Conner and Adkisson 1976, Whitmore 1981). Mathematically (DFA) it is possible to maximally separate two groups of multivariate observations with a single axis (Harner and Whitmore 1977). A line drawn in three or n-dimensional space can easily be positioned to intersect two multivariate means (centroids). If three or more centroids for species are analyzed simultaneously, a single line can no longer intersect all centroids unless a perfectly linear relationship exists for the species being examined. The probability of such an occurrence is extremely low. Thus, a high degree of resolution can be realized when a two-group DFA is used to determine habitat parameters important to individual species. We have used two-group DFA to identify vegetation variables important to 12 common species of songbirds in East Texas.

METHODS

Four pine and four pine-hardwood stands representing growth stages from small sapling to sawtimber were selected for bird and habitat sampling. All stands were in the loblolly pine (Pinus taeda)-shortleaf pine (P. echinata)-hardwood forests of East Texas within an 80-km radius of Nacogdoches. Stands are described more completely in Dickson and Segelquist (1979) where the same bird data used in this study were used to examine bird diversity and density in relation to foliage layers.

A 10-ha study area within each stand was delineated away from adjoining habitats to
### Table 1

**Habitat Variables for 12 Songbirds in East Texas Pine and Pine-Hardwood Forests**

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Code</th>
<th>Bird species</th>
<th>Code</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation height (m)</td>
<td>VEGHT</td>
<td>Carolina Chickadee</td>
<td>CCHK</td>
<td>37</td>
</tr>
<tr>
<td>No. shrub species</td>
<td>NSRSP</td>
<td>(Parus carolinensis)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. tree species</td>
<td>NTRSP</td>
<td>Tufted Titmouse</td>
<td>TUF</td>
<td>50</td>
</tr>
<tr>
<td>No. shrub stems</td>
<td>SRDEN</td>
<td>Brown-headed Nuthatch</td>
<td>BHNH</td>
<td>21</td>
</tr>
<tr>
<td>% canopy closure</td>
<td>CANCL</td>
<td>Carolina Wren</td>
<td>CWRN</td>
<td>81</td>
</tr>
<tr>
<td>Foliage density at 1 m</td>
<td>FOLDN1</td>
<td>(Sitta pusilla)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foliage density at 3 m</td>
<td>FOLDN3</td>
<td>(Thryothorus ludovicianus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foliage density at 7-10 m</td>
<td>FOLDN8</td>
<td>White-eyed Vireo</td>
<td>WEV</td>
<td>65</td>
</tr>
<tr>
<td>Foliage density above 20 m</td>
<td>FOLDN20</td>
<td>(Vireo griseus)</td>
<td>REV</td>
<td>26</td>
</tr>
<tr>
<td>% hardwoods 5-16 cm DBH</td>
<td>PHDW1</td>
<td>(V. olivaceus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% hardwoods 17-32 cm DBH</td>
<td>PHDW2</td>
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<tr>
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<tr>
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</table>
| *N = number of grid points for habitat used by each bird species.*

minimize edge effect. Forty-six to 49 systematically located grid points (50 m between points) were established in each study area. Birds in the eight study areas were censused by spot-mapping (International Bird Census Committee 1970) from 1 April-8 June 1975 using the grid points to maintain plotting accuracy. Data with sufficient sample sizes (at least 21 grid points of vegetation measurements per species and more than 10 different individual birds per species) for analyses were collected for 12 species of birds (Table 1).

Vegetation measurements were made at each of the grid points in all study areas (Table 1). Foliage density from the ground to 3 m height was measured with a 0.5 × 0.5-m gridded board (MacArthur and MacArthur 1961). Foliage density at 7-20 m from the ground was measured by sighting vertically through a 400 mm telephoto lens on a reflex camera over each grid point (MacArthur and Horn 1969). Foliage density higher than 20 m was estimated from the proportion of the vertically directed camera lens unobscured by foliage above 20 m.

Density and diameter of trees over 5 cm DBH were measured on 10 × 10-m plots. Density
of woody plants less than 5 cm in diameter and over 30 cm high was measured on 2 × 2-m plots at the 382 sample points.

Territories of singing males determined from census data were superimposed on the eight study area maps containing grid points. Vegetation measurements at points falling within the territory boundaries of males of a species were considered habitat used by that species and were compared, using a two-group DFA, with vegetation measurements for grid points not included in the territories. (See Table 1 for sample sizes: number of grid points of used habitat [N] plus number of grid points not included in species territories = 382.) One analysis was calculated for each of the 12 bird species. Prior probabilities for classification functions were adjusted for differences in group sample sizes. All 12 DFAs were significant (Mahalanobis D square, similar to a MANOVA, \( P < 0.05 \)).

We calculated the correlation of the original vegetation variables to the discriminant axis (canonical variate) for each species (Timm 1975, Dueser and Shugart 1978). We used this technique because it evaluates the importance of each variable to the discrimination independent of intercorrelations among the original variables. Although we have used the \( P < 0.01 \) as a cut off level for inclusion of correlations (Table 2), significance level should not be the main criterion to evaluate the correlations; the direction and relative magnitude are more meaningful (Timm 1975).

A 12-group DFA was calculated with vegetation measurements of each bird species as a group. We compared results of this community ordination with the individual results of the two-group DFAs to see which provide a higher degree of habitat resolution and classification success (Tables 3 and 4).

Calculation of two-group DFAs for habitat classification (Table 5) was accomplished by using stepwise DFA which allowed only certain variables to enter (F to enter and be removed was 1.5—see BMDP7M, Dixon 1974). Intercorrelations among variables resulted in differences in the sets of variables entered in Table 5 and Table 2 in each species category.

Violation of the assumption of homogeneity of group dispersions (heterogeneity of variance-covariance matrices) is a matter of increasing concern with the application of DFA to habitat studies (Williams 1981). Because of the high probability of an inequality of group dispersions resulting from unequal group sample sizes, we recalculated all 12 DFAs again after log transformation of the data. DFAs with the log transformed data supported the original analyses completely. There was no change in either the direction or relative magnitude of the correlations of original variables to the 12 discriminant functions. Thus, we considered the original analyses to be acceptable (Pimentel 1979).

Evaluating the importance of habitat variables for species by two-group DFA has a potential problem. If a bird does not occupy one extreme of the habitat for at least one variable, the analysis and subsequent correlations to the discriminant axis may not be significant. Thus, habitats of species favoring "middle" portions on all habitat gradients are difficult to quantify with DFA. Also, interspecific territoriality may force a subordinate species to use sub-optimal habitat. In such a case, the accuracy of a DFA to indicate a species' preferred habitat would be reduced. Many territories of the bird species we studied overlapped within study areas. Thus, we did not notice any obvious examples of interspecific territoriality.

RESULTS AND DISCUSSION

Comparison of two-group and 12-group DFA.—A three dimensional ordination of the 12 species following the 12-group DFA revealed four general aggregations of bird species (Fig. 1). Pine Warblers and Brown-headed Nuthatches formed one group representing species using mature pine forests (Table 3). Prairie Warblers and Yellow-breasted Chats formed an
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* See Table 1 for samples sizes of habitat used by each species.
aggregation of species using early succession vegetation. Black-and-white Warblers, Red-eyed Vireos, Tufted Titmice, and Carolina Chickadees formed a third aggregation of species using relatively mature pine-hardwood forest vegetation with the latter of the four species using pines more often. The general vegetation requirements of the above eight species can be inferred from the ordination (Fig. 1) and correlations of original variables to the first three discriminant functions (Table 3). However, the detail and ranking of each original variable’s importance to individual species are not as clear with the 12-group analysis (Table 3) as they are with the 12 two-group DFAs (Table 2).

The fourth aggregation of species from the 12-group DFA demonstrates the poor resolution even more (Fig. 1). A description of the vegetation requirements of the White-eyed Vireo, Northern Cardinal, Indigo Bunting,

---

**Table 3**

**Correlations of Original Variables to the First Three Axes in a 12-Group DFA Calculated on Combined Data of 12 Species of Common Songbirds in Eastern Texas**

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Cumulative % of variation explained

- 54.2
- 82.0
- 87.2

*See Table 1 for variable codes.*
TABLE 4
PERCENTAGES OF CORRECT CLASSIFICATIONS OF BIRD SPECIES BY TWO-GROUP AND SEVERAL-GROUP DFA

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<td>Mean percentage correctly classified</td>
<td>74.0%</td>
<td>30.5%</td>
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*See Table 1 for species codes.*

and Carolina Wren based on the results of the 12-group DFA would mask any special vegetation requirements of individual species. Results from the two-group DFAs provide detailed descriptions of the requirements of each species and clearly demonstrate differences among the four species (Table 2).

Comparison of the percentages of cases correctly classified by the 12-group versus two-group DFAs further demonstrates the accuracy of the two-group analyses (Table 4). In all species the percentage of correctly classified cases was higher with the two-group DFAs than with the 12-group DFA.

Two-group DFA bird-vegetation associations.—Several bird species were associated with low shrubby vegetation. White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were in general positively associated with increasing density of shrub stems (SRDEN), foliage density from 0–1 m high (FOLDN1), percent sapling pines (PPIN1), and number of shrub species (NSRSP) (Table 2). These four bird species were negatively associated with increasing vegetation height (VEGHT), percent canopy closure (CANCL), foliage density 12–15 m (FOLDN13), percent of pole-size pines (PPIN2), and density of all pole-size trees (TRDN2). The number of tree species (NTRSP) was apparently not important to these early succession species. Northern Cardinals, Yellow-
Table 5
Unstandardized Discriminant Function Coefficients, Constants, and Group Means for Songbird Habitat in East Texasa

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Group means

| Used habitat |     | .6997| 1.4355| 1.6805| .5637| 1.0075| .6634| .7106| 1.2590| .9340| 1.0555| 1.1938| 1.7695  |
| Unused hab.  |     |-.1430| -.1815| -.1073| -.1912| -.0764| -.1779| -.0760| -.0917| .1119| -.1584| -.2623| -.1026  |

See Table 1 for sample sizes of habitat used by each species.
Fig. 1. Three dimensional ordination of a 12-group DFA on common East Texas songbirds. The first function (left to right) represents a transition from young clearcuts to mature forests. The second function (back to front) represents increasing tree and shrub species diversity. See Table 4 for correlations of original variables to axes and Table 1 for bird species codes.

breasted Chats, and White-eyed Vireos were positively associated with increasing foliage densities at 3 m (FOLDN3), as well as 1 m, above the ground and favored later phases of the early successional stage more than Prairie Warblers.

The above four bird species regularly use low, shrubby vegetation in other geographic areas. In Georgia, the same four species occurred in the grass-shrub stage of succession (Johnston and Odum 1956). Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were common breeding birds in 3-, 7-, and 12-year-old mixed oak stands in Virginia (Conner and Adkisson 1975), and the White-eyed Vireo occurred in the 7-year-old stand. In Arkansas, Prairie Warblers and Yellow-breasted Chats were characterized as open-country birds, and White-eyed Vireos inhabited shrubs and low trees (James 1971). In East Texas, Northern Cardinals and White-eyed Vireos are ubiquitous and often occur in mature forests as well as clearcuts (Dickson and Segelquist 1979). In mature forests they probably occur where openings in the canopy permit shrub level vegetation.

Red-eyed Vireos, Black-and-white Warblers, and Tufted Titmice were associated with mature forest stands and were positively associated with increasing number of tree species, vegetation height, percent canopy closure, percent of sapling hardwoods (PHDW1), large tree density (TRDN3), and number of shrub species (Table 2). The three bird species were neg-
atively affected by increasing percentages of sapling pines (i.e., young pine stands). In a study in Georgia, these three bird species were found only in the three oldest stands (Johnston and Odum 1956). In Arkansas they were typical inhabitants of well-developed shaded forests (James 1971). In another investigation in Arkansas, all had strong positive correlations with large trees, percent canopy cover, and average tree height (Smith 1977).

These three mature forest birds were also positively associated with increasing foliage density at 7–10 m (FOLDN8), 12–15 m (except Black-and-white Warblers) and above 20 m (FOLDN20). This association would be expected with Red-eyed Vireos as they are canopy gleaners (Williamson 1971). Anderson and Shugart (1974) found that Red-eyed Vireos were positively correlated with canopy biomass and subcanopy tree size.

Pine Warblers and Brown-headed Nuthatches were favored by mature stages of pine forests. Pine Warblers had strong positive associations with increasing percent of pole-size pines and vegetation height (Table 2). They avoided areas with dense sapling stage pines. The number of tree and shrub species, as well as foliage density at different heights, had little importance to Pine Warblers. Johnston and Odum (1956) found these birds in all their sampled pine stands from 25–100 years old. Anderson and Shugart (1974) noted the species frequented areas with a dense canopy and sparse understory. Brown-headed Nuthatches had a strong preference for pole stage pure pine stands. They were strongly associated with increasing percent of pole-size pines and negatively associated with increasing number of shrub species, number of tree species, and density of sapling stems (TRDN1) (Table 2). In Georgia, Johnston and Odum (1956) found them in the oldest pine stands. They noted that Pine Warblers, Brown-headed Nuthatches, and Red-cockaded Woodpeckers (Picoides borealis) were the only breeding species generally restricted to southern pines.

Indigo Buntings were somewhat similar to early succession species; however, they showed no relationship with vegetation height, number of shrub species, and density of shrub stems (Table 2). They were positively associated with increasing percentage of sapling pines, and negatively associated with increasing density of pole-size trees (TRDN2), density of foliage 7–15 m, number of tree species, and percent canopy closure. Indigo Buntings could apparently tolerate tall vegetation as long as it was sparse, i.e., very patchy. The absence of tall trees did not affect the bunting negatively. Indigo Buntings are sometimes abundant in both middle-aged and young shrubby stands in the south (Shugart and James 1973, Conner and Adkisson 1975, Strelke and Dickson 1980).

Carolina Wrens had strong positive associations with increasing number of shrub species, number of shrub stems, and percent sapling hardwoods
(Table 2). They were adversely affected by increasing density of pole-size trees and percent pines of pole size. Dense pole stands probably impeded light penetration and inhibited dense and diverse shrub level vegetation. Carolina Wrens, like Northern Cardinals and White-eyed Vireos, were found in a wide range of stand heights, but inhabited the shrub layer of vegetation. Carolina Wrens were positively associated with shrub level vegetation in Arkansas (James 1971) and Louisiana (Dickson and Noble 1978).

Carolina Chickadees preferred areas with open understories. They were negatively associated with increasing number of shrub species, shrub density, percent pine saplings and sapling density. They were positively associated with foliage density 12–15 m and percent of pole-size pines. Carolina Chickadees inhabited this pine and hardwood subcanopy, and the dense subcanopy probably shaded sufficient light to minimize understory growth beneath. Chickadees were found predominantly in the canopy of a mature hardwood forest in Louisiana (Dickson and Noble 1978), and in Georgia they inhabited the four oldest stands (Johnston and Odum 1956). In Virginia they inhabited two young stands (Conner and Adkisson 1975) and they were abundant in woods-clearcut edge in East Texas (Strelke and Dickson 1980). In Tennessee they also preferred habitat with open understories (Anderson and Shugart 1974).

Habitat classification.—Discriminant function analysis can be used to determine whether vegetation in different parts of a forest is suitable for a particular bird. Unstandardized discriminant function coefficients and constants (Table 5) can be used to calculate values that in turn can be used to evaluate the suitability of a particular forest area to the 12 bird species we studied.

The equation needed to evaluate each species is:

\[
D = b_1X_1 + b_2X_2 + b_3X_3 + \ldots + b_iX_i + K
\]

where \(D\) = the discriminant score needed to evaluate the species, \(b\) = the coefficients for each species' variables, \(X\) = the values for field measured habitat variables, and \(K\) = a constant for each species.

The discriminant score (D) is compared to a linear scale of the mean for habitat used by the species and the mean for habitat not used by the species. The closer the discriminant score is to the mean for used habitat, the more favorable the habitat is to the bird species being tested. Generally, the habitat in question would be considered favorable to the bird species if the discriminant score were greater than the midpoint between the means of the used and unused habitats (Conner and Adkisson 1976).

The habitat classification functions for only the White-eyed Vireo, Yellow-breasted Chat, Indigo Bunting, and Red-eyed Vireo were tested with
vegetation data collected in spot-mapped territories for each of these species during 1980. Data for the tests were collected on an area different from the original eight study areas. The averages of vegetation variables measured at three randomly located points within one territory of each species were used as input data for the habitat classifications. For example in the case of the Red-eyed Vireo \((b \times X_i)\):

\[
\begin{align*}
\text{NSRSP:} & \quad 0.1201 \times 4.33 = 0.5200 \\
\text{NTRSP:} & \quad 0.2265 \times 4.0 = 0.9060 \\
\text{CANCL:} & \quad 1.2002 \times 0.9433 = 1.1321 \\
\text{PPIN1:} & \quad -0.9368 \times 0.0 = 0.0
\end{align*}
\]

The sum of these products plus the constant \((K = -0.8559)\) provides the discriminant score \((D = 1.7022)\). For the Red-eyed Vireo the mean for the used habitat is 1.2590 and for the unused habitat \(-0.0917\) (Table 5). Thus, the calculated discriminant score is much closer to the mean for habitat used by this species than the mean for habitat not used, and the area being tested would be correctly classified as habitat suitable for Red-eyed Vireos.

Discriminant scores calculated for the White-eyed Vireo \((D = 2.1603)\), Yellow-breasted Chat \((D = 1.6045)\), and Indigo Bunting \((D = 0.4782)\) were closer to the mean for habitat used by the species than habitat not used (Table 5) and thus were all correctly classified.

MANAGEMENT RECOMMENDATIONS

Clearcutting in mixed pine-hardwood forests of East Texas provides excellent habitat for early succession bird species, such as White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, Northern Cardinals, and Indigo Buntings. Cuts 10-20 ha would be sufficient to contain at least several territories for each species. Buntings and Northern Cardinals also prefer some tall live or dead trees for singing perches. These birds need foliage 1-3 m above the ground for both foraging substrate and nest concealment. Indigo Buntings, however, would probably be tolerant of stands with low foliage density at 1 and 3 m. Shrub species diversity and stem density should be kept reasonably high to provide habitat for all of the five bird species. These requirements preclude or minimize the use of herbicides to eliminate young sprouting hardwoods. Clearcutting should provide high quality habitat for the birds for about 2-8 years after cutting.

Carolina Wrens, White-eyed Vireos, and Northern Cardinals inhabit shrub-level vegetation in stands of a wide variety of tree heights. In young pine stands, habitat for these birds could be enhanced by avoiding timber stand improvement (TSI, killing unwanted hardwoods), by planting with wide spacing such as 3.6 \(\times\) 3.6 m (12 \(\times\) 12 feet) and by avoiding intensive
site preparation measures such as KG blading and chopping. In old pole and mature stands, frequent thinnings and selected tree injection or girdling should enhance shrub vegetation.

Red-eyed Vireos, Black-and-white Warblers, and Tufted Titmice selected more mature forest stages. Later stages of forest succession (30–60 years following clearcutting), when trees are tall and at least a partly deciduous canopy is present, should provide high quality habitat. Since these three species used habitat with increasing tree species diversity, TSI should be avoided. Johnston and Odum (1956) and Dickson and Seigelquist (1979) have pointed out the importance of deciduous foliage in pine stands to birds.

Carolina Chickadees, Pine Warblers, and Brown-headed Nuthatches selected pine pole stands and mature pine forests. Brown-headed Nuthatches in particular would benefit from management that provided mature stands of mostly pines. These three species would be negatively affected by clearcutting for perhaps 12–25 years.

**SUMMARY**

In 1975, 12 breeding bird species were spot-mapped in four pine stands of different heights and four comparable sized pine-hardwood stands. Vegetation measurements were made at 382 grid points within the eight stands. Vegetation at grid points within each species’ territories was compared to vegetation not included in territories using a separate two-group discriminant function analysis (DFA) for each species. Correlations of original variables to the 12 DFA axes were calculated to determine which vegetation parameters were important to individual bird species. When compared to a single 12-group DFA, the two-group DFAs provided a more detailed description of individual species’ vegetation requirements. Early succession bird species such as White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were positively associated with increasing density of shrub stems, foliage volume at 1 and 3 m high, percent sapling pines, and number of shrub species and negatively associated with increasing vegetation height, canopy closure, and number of pole-size trees. Late succession bird species such as Red-eyed Vireos, Black-and-white Warblers and Tufted Titmice favored increasing vegetation height, number of tree species, and canopy closure. Other bird species had their own specific vegetation requirements.

**ACKNOWLEDGMENTS**

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RECENT CHANGES IN RING-BILLED AND CALIFORNIA GULL POPULATIONS IN THE WESTERN UNITED STATES

MICHAEL R. CONOVER

Bent (1921) noted the decline of the Ring-billed Gull (Larus delawarensis) population since the 1840s, a phenomenon which he attributed to the intolerance of this species to disturbances at its breeding colonies. By the 1920s the Ring-billed Gull’s breeding range, which previously extended across most of North America as far east as the Atlantic Ocean, had become restricted to lakes in the remote, unsettled regions of the western states and Canadian provinces. There, Bent (1921) believed, the Ring-billed Gull population was holding its own, except where encroached upon by expanding civilization.

The human population has greatly increased in the western United States and Canada since Bent’s time and many formerly remote areas have now been settled. Whether this human settlement and the resultant environmental changes have had the deleterious impact on Ring-billed Gulls that Bent (1921) feared is uncertain. However, two studies of ring-bills, focusing on limited areas, have shown recent population growth in this species. Ludwig (1974) documented a large increase in the gull population of the Great Lakes. Conover et al. (1979) reported a similar population increase during this century of Ring-billed and California gulls (L. californicus) in the state of Washington.

Nonetheless, it is uncertain from these reports if population increases are local phenomena or are widespread throughout the breeding range. For this reason, I sought to determine the size of the current breeding populations of Ring-billed and California gulls in the western United States and to compare them to records of population size at the beginning of the 20th Century.

Man has been responsible for several environmental changes in the West during the present century which may have affected the Ring-billed Gull and California Gull populations by altering their food resources or nesting habitat. These changes include the creation of large water impoundments, the expansion of towns and cities with their garbage dumps, and the advent of large-scale farming. In addition, this study assesses any beneficial effects these changes may have had for the gulls by allowing them to establish new breeding colonies or expand existing ones.

METHODS

The area studied included the 17 western states, roughly encompassing the western half of the continental United States (Fig. 1). This area represents 30–40% of the total breeding
range of the Ring-billed Gull and about 50% of that of the California Gull (see Vermeer 1970). This region was thinly settled until the late 19th and early 20th centuries, thus providing an opportunity to evaluate man's impact on the population of these two gull species.

In a previous study (Conover and Conover 1981), the breeding populations of Ring-billed and California gulls during the 1920s were estimated from a literature survey of reports of gull colonies in the western U.S. before 1930. Breeding populations of these two species in the 1920s were estimated from total counts of breeding gulls from each colony for which population data were available. For colonies censused repeatedly, I used the population survey made closest to 1930. For those few colonies of undetermined size, I substituted the mean number of gulls per colony for colonies of known size.

To assess the 1980 Ring-billed and California gull breeding populations, I needed to determine the location and size of existing colonies. These data were obtained from my observations, published reports, the Colonial Bird Register, and by contacting state wildlife departments, national wildlife refuge managers, colleges and universities, cooperative wildlife and fisheries units, ornithologists, and Audubon groups. I estimated the current breeding population of each species as I had for the breeding population in the 1920s.

The construction of large reservoirs, establishment of towns and cities, or the advent of large-scale agriculture may have facilitated formation of new colonies through creation of new areas with adequate food resources and protection from mammalian predators. For each newly-reported colony, I examined any man-made environmental changes in the immediate vicinity. For example, to assess the importance of reservoirs, I counted the number of new colonies located on impoundments. To evaluate the potential effect of an expanding human population, I first examined census records (U.S. Census Bureau 1975) to document human population increases in the western U.S. since 1850. I also counted the number of colonies that were within 12, 24, or 36 km of towns by plotting them on maps of the U.S. Geological Survey (1970) which also provided data on the population of each town. These distances were selected because I found that, at least in Washington, most individuals of both species fed within 12 km of the colony with a few ranging to 36 km (Conover, pers. obs.). To ascertain if location of colonies in 1980 was non-random with respect to proximity to towns, I determined how frequently colonies were located within 36 km of a town with a population >1000. I then compared this frequency to the frequency of randomly-selected points which were also located within 36 km of a town having >1000 residents. These points were randomly placed on a map of the breeding range of these gulls in the western U.S. I then used a contingency table corrected for continuity to test for significant differences ($P < 0.05$) in the proportion of colony sites and random sites which were near towns.

I also used census records (U.S. Census Bureau 1975) to calculate any changes in farm acreage and irrigated farm acreage in the West since 1850. I then determined how many of the 1980 gull colonies were within 36 km of an area where the principal land use was either for cropland or for irrigated cropland, using maps from the U.S. Geological Survey (1970). This frequency was then compared to the frequency of randomly-selected points also near agricultural areas. By using a contingency table corrected for continuity, I was able to determine if the location of colonies was non-randomly distributed with respect to agricultural areas and areas of extensively irrigated farmland.

**RESULTS**

The sizes and locations of colonies of these two gulls in the western U.S. during the 1920s and in the 1970s are given in Appendix 1 and 2, respectively. During the 1920s, 17 California and 16 Ring-billed gull colonies were reported in the West (Figs. 1, 2). Reports of two California Gull and four Ring-billed Gull colonies based on second-hand information
were regarded as questionable. Although Dawson (1923) mentioned California Gulls nesting on Lake Tahoe and along the Sacramento River he never actually visited those locales. I found no other references to these alleged colonies. There are some California Gull eggs in the collections at the Museum of Vertebrate Zoology (Univ. California) possibly collected along the Sacramento River (Grinnell and Miller 1944). Reports of Ring-billed Gull colonies on the Belly River, Flathead River, McDonald Lake, and St. Mary's Lake in Montana may also be spurious (Bailey 1918). Bailey (1918) apparently did not visit these sites himself and I could find no other evidence of the existence of these colonies. The absence of additional
reports suggests that if these alleged colonies did exist, they probably were occupied for only a few years. Thus, only 15 or so *L. californicus* colonies and 12 *L. delawarensis* colonies apparently existed in the western U.S. during most of the 1920s.

In 1980, Ring-billed Gulls nested in 57 colonies (Fig. 3), an increase of 356–475% depending on the inclusion of questionable pre-1930 colonies. Available population data from 83% of the pre-1930 colonies (Appendix 1) indicated that before 1930, the mean number of breeding Ring-billed Gulls per colony was 397. Hence, based on 12 colonies, the total known Ring-billed Gull population in the western U.S. prior to 1930 was 4800. In 1980,
the mean number of breeding Ring-billed Gulls per colony was 1867, a five-fold increase in mean colony size since 1930. Thus, the Ring-billed Gull population in the western U.S. was about 106,000, some 22 times larger than the apparent population in the 1920s.

In 1980, California Gulls nested in 80 colonies (Fig. 4). This was 471–533% higher than in the 1920s depending on the inclusion of questionable pre-1930 colonies. The mean number of breeding California Gulls per colony prior to 1930 was 6734 based on data from 93% of the early colonies. Thus, based on 15 colonies, the pre-1930 population of California Gulls in
the western U.S. was 101,000. In 1980, the mean number of breeding California Gulls was 3455, a decrease of 51% in colony size since 1930. Hence, the current California Gull population in the western U.S. was approximately 276,000, 2.7 times larger than before 1930.

Much of the increase in California Gull numbers has occurred in the northern states. The number of colonies in Washington rose from 1 to 11, in Idaho from 1 to 10, in Montana from 2 confirmed colonies to 18, and in North Dakota from 5 to 17. By 1980, California Gulls were still nesting in only 8 of 17 colony sites dating from the 1920s and Ring-billed Gulls only occupied 6 of 12 earlier sites.
Surprisingly, before 1930 over 80% of the total California Gull breeding population in the western U.S. was centered on Great Salt Lake in Utah. Then the number of breeding gulls on this lake declined from around 82,800 in 1932 to only 41,000 in the late 1940s (Behle 1958). The estimated population of 50,000 in 1980 shows a slight increase over the late 1940s but falls far short of the 1932 estimated total. Elsewhere in the western U.S., California Gull populations have increased from an estimated 18,210 in the 1920s to 226,000 in 1980.

The creation of reservoirs throughout the western U.S. has certainly contributed to, though not solely caused by, the growth of these gull populations. Of Ring-billed and California gull colonies established in the western
U.S. since 1930, 33% were located in new breeding habitat on man-made reservoirs.

Also of probable importance to the gull population increases in the West has been the burgeoning of human settlements with associated garbage dumps providing new sources of food (Fig. 5). Many of the 1980 colonies were near towns or cities: 84% were within 36 km of a town with >1000 people and 40% were within 36 km of a town with >10,000 inhabitants (Table 1). Only 45% of the randomly-selected locations were within 36 km of a town with a population exceeding 1000. This was significantly lower ($\chi^2 = 28.69$, df = 1, $P < 0.001$) than for gull colonies, indicating that gull colonies were not randomly located with respect to human settlement.

Furthermore, increased farm acreage in the western U.S. since the 1900s (Fig. 6) has also expanded potential food sources for gulls; in fact, 96% of the colonies in 1980 were situated within 36 km of areas where the main land use was for agriculture. This also was significantly higher ($\chi^2 = 15.19$, df = 1, $P < 0.001$) than the 75% of randomly-selected locations near agricultural areas. In particular, irrigated farmland in the western U.S. increased from 1,500,000 ha in 1890 to 5,700,000 ha in 1930 and to 14,200,000 ha in 1970 (U.S. Census Bureau 1975). In 1980, 74% of the colonies were located within 36 km of an area with extensive irrigated cropland, although only a small fraction of the total farm acreage was irrigated. This frequency was significantly greater ($\chi^2 = 18.44$, df = 1, $P < 0.001$) than the 41.3% of random locations which were near irrigated farmland. This association of gull colonies with irrigated acreage was particularly strong in the Pacific Northwest in contrast to the situation in eastern Montana, Colorado, North Dakota, and South Dakota where there was little irrigated farming. Outside this latter area, 95% of the new colonies were within 36 km of extensive areas of irrigated cropland.

**DISCUSSION**

**Accuracy of the population estimates.**—Total accuracy in the population estimates is difficult to achieve for several reasons. Colonies may have
been missed, making the population estimates conservative. However, the last 20 reports of gull colonies which were received contained only one new colony suggesting that only a small percentage of colonies may have been overlooked. Any error stemming from missed colonies, would likely have a greater effect on pre-1930 population estimates because there were fewer ornithologists then. Conversely, there may be an overestimation of the total number of colonies in existence prior to 1930, because some reported colonies were undoubtedly deserted in any one year. Whether these two factors counter-balance each other is unclear. Yet another source of error has resulted from observers estimating rather than counting numbers of birds both in current and pre-1930 colonies. For most of the pre-1930 colonies, however, there were at least two independent estimates of colony size (Conover and Conover 1981). Given these limitations, the population figures should be regarded as minimum estimates.

_Reasons for the population changes._—Increases in Ring-billed and California gull populations in the western U.S. may have been influenced by
two developments similar to those causing the Ring-billed Gull population growth in the Great Lakes: the use of new food sources and the creation of suitable breeding habitat (Ludwig 1974). Food sources and breeding habitat have increased in these two areas for different reasons. In the Great Lakes, new breeding habitat was created during a period of low water, which exposed new islands (Ludwig 1974), but in the West, many new colonies are now located on islands in new reservoirs. This creation of islands has allowed gulls to establish new colonies in areas which previously lacked suitable breeding sites. Likewise, the establishment of alewives (Alosa pseudoharengus) in the Great Lakes provided a new food source for gulls (Ludwig 1974). In the West gulls have exploited new terrestrial food sources created by man, e.g., garbage dumps and other sources of human refuse. Modern agriculture has also created new food sources used by Ring-billed and California gulls. The proximity of contemporary colonies to large agricultural areas suggests the potential importance of agricultural food supplies for California and Ring-billed gulls.

Apparently farming based on irrigation has especially benefitted these gulls. Conover et al. (1979) noted that these gulls in eastern Washington spent more time feeding in irrigated than non-irrigated fields, although the latter greatly outnumbered the former in acreage. Baird (1977) also reported that Ring-billed Gulls in Montana foraged mainly in irrigated fields, with California Gulls feeding more in the plains and non-irrigated fields. Throughout the Pacific Northwest in 1980, most colonies were near areas with extensive irrigated farmland.

Agricultural fields may be a more important food source for Ring-billed and California gulls than garbage dumps and human settlements. Vermeer's (1970) extensive study in Alberta revealed that rodents, insects, and grain (types of food gulls gather from cultivated fields) were the principal components of most food samples. Garbage rarely comprised more than 5% of the food samples collected in May and June, although in some areas, its importance increased in July. Other studies of food habits in the Great Lakes (Jarvis and Southern 1976, Haymes and Blokpoel 1978), Montana (Rothweiler 1960), California (Anderson 1965), and Utah (Greenhalgh 1952) have shown that insects were an important part of the diet of these gulls. It would appear that garbage was less important even though two of these studies (Greenhalgh 1952, Haymes and Blokpoel 1978) were conducted near large urban areas.

Perhaps the Ring-billed Gull population has increased more than the California Gull in the western United States, in part, because of the different food habits of the two species. Ring-billed Gulls feed more in upland areas than do California Gulls; ring-bills consume more insects and grain, whereas California Gulls eat more carrion and garbage (Rothweiler 1960,
Anderson 1965, Vermeer 1970). Consequently, any increase in the availability of grain and insects might well have a greater influence on Ring-billed Gulls than California Gulls. The increase in farming activities would create such a situation.

Also contributing to the Ring-billed and California gull population growth is reduced predation pressure, although to what extent is unclear. Certainly man poses less of a threat to these gulls today; gulls are no longer killed for their plumage nor are their eggs regularly taken for food although at present gulls are probably disturbed more by human activities in their breeding colonies and by senseless shootings.

Ring-billed and California gulls are not the only species that have increased in numbers in the 20th Century. Other gull species also increasing during this century include the Great Black-backed Gull (L. marinus) in New England (Drury 1973); the Dominican Gull (L. dominicanus) in Wellington, New Zealand (Fordham 1967, 1970); the Lesser Black-backed Gull (L. fuscus) in Britain (Parslow 1967, Harris 1970); and the Herring Gull (L. argentatus) in both Europe (reviewed by Spaans 1971) and North America (Kadlec and Drury 1968, Drury 1973). These increasing populations have usually been attributed to reduced predation and exploitation of garbage dumps as a food source. Recently, the population of some of these gull species has stabilized (Fordham 1970, Drury and Kadlec 1974).

Whether Ring-billed and California gull populations will continue to increase is unpredictable, especially given the growing demands for recreational or commercial use of lakes and islands where these gulls breed. For instance, the large colony of California Gulls at Mono Lake may eventually be threatened by Southern California’s increasing need for water. The population explosion of these gulls has had some harmful repercussions, such as increased depredation on the eggs and young of waterfowl (Odin 1957, Vermeer 1970), damage to cherry orchards (Behle 1958), and increased danger of collisions with aircraft (Blokpoel 1976). However, given the benefit which these two gull species provide farmers in reducing the insect and rodent populations in their fields (see Behle 1958), and their beauty and aesthetic value, any further increase in population should be encouraged whenever local conditions permit.

SUMMARY

During the last 50 years, the Ring-billed Gull (Larus delawarensis) breeding population in the western United States has increased from a minimum of 4800 to 106,000 individuals in 1980. This increase, approximately 22-fold, is manifested in two forms: an increase in mean colony size from 397 to 1867 breeding adults and a proliferation of colonies from 12 to 16 in the 1920s to 57 today. Concomitantly, the breeding population of California Gulls (L. californicus) in the western U.S. has more than doubled, from ca. 101,000 to 276,000 in 1980. Interestingly, while the number of California Gull colonies has increased from 15 in 1930 to 80 in 1980, the
mean number of gulls per colony has decreased, from 6734 to 3455 during the same period. Both gull species have apparently benefited from increased food supplies resulting from edible human garbage and agricultural practices. Also aiding the proliferation of these gulls has been the creation of new nesting habitat on islands formed by large reservoirs and the reduction of human predation by egg and plumage hunters.

ACKNOWLEDGMENTS

I thank the National Audubon Society Research Department and the Cornell Laboratory for the use of data contained in the Colonial Bird Register. I also thank the numerous people listed in the appendices who contributed data on current gull populations. D. Aylor, D. Conover, D. Schneider, and G. Hunt provided helpful comments on the manuscript.

LITERATURE CITED


Conover - GULL POPULATION CHANGES


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**APPENDIX 1**

RING-BILLED GULL AND CALIFORNIA GULL Colonies in Western U.S. during the 1920s

<table>
<thead>
<tr>
<th>State</th>
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<td>1800</td>
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<td>4</td>
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<td>Ray (1915, 1921), Grinnell et al. (1930)</td>
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<tr>
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<td>300</td>
<td>Moffitt (1942)</td>
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<tr>
<td></td>
<td>Mono Lake</td>
<td>3400</td>
<td>—</td>
<td>Dawson (1923), Grinnell and Storer (1924)</td>
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<tr>
<td></td>
<td>Sacramento River</td>
<td>breeding</td>
<td>—</td>
<td>Dawson (1923), Grinnell and Miller (1944)</td>
</tr>
<tr>
<td></td>
<td>Tahoe Lake</td>
<td>breeding</td>
<td>—</td>
<td>Dawson (1923)</td>
</tr>
<tr>
<td>Nevada</td>
<td>Pyramid Lake</td>
<td>14</td>
<td>—</td>
<td>Hall (1926), Gromme (1930)</td>
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<tr>
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<td>Malheur Lake</td>
<td>3500</td>
<td>1000</td>
<td>Willett (1919), Gabrielson and Jewett (1940)</td>
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## APPENDIX 1
### CONTINUED

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<td>—</td>
<td>20</td>
<td>Saunders (1921)</td>
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<td>Bowdoin Lake</td>
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<td>1000</td>
<td>Willett (1907), Weydemeyer and Marsh (1936)</td>
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<td>Hayward (1935), Behle (1945)</td>
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<td>320</td>
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<td>330</td>
<td>Stevens (1930)c, Stewart (1975)</td>
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<td>Stump Lake</td>
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<td>400</td>
<td>Bent (1921), Wood (1923), Stewart (1975)</td>
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* Western states not listed had no known colonies.

b As cited by Behle (1936).

c As cited by Stewart (1975).
## Appendix 2
### Recent California Gull and Ring-billed Gull Colonies in the Western U.S.

<table>
<thead>
<tr>
<th>Colony name (county)</th>
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<td>breeding</td>
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<td>1977</td>
<td>15</td>
<td>100</td>
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<td>breeding</td>
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<td>400</td>
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<td>1690</td>
<td>5436</td>
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<td>Ring-billed Gull</td>
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*Note: The values in the table represent the number of gulls observed. Breeding indicates that nesting was observed.*
### APPENDIX 2

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### APPENDIX 2

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**CONTINUED**

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* C.B.R.—Colonial Bird Register.
JAMAICA BAY STUDIES: IV. ABIOTIC FACTORS AFFECTING ABUNDANCE OF BRANT AND CANADA GEESE ON AN EAST COAST ESTUARY

JOANNA BURGER, RICHARD TROUT, WADE WANDER, AND GLEN RITTER

Most Brant (Branta bernicla) and Canada Geese (B. canadensis) breed in northern Canada, although Canada Geese also nest in some areas of the United States. During the breeding season Brant and other geese are terrestrial grazers. In the non-breeding season Canada Geese continue to eat terrestrial plants and seeds. However, Brant switch to feeding on submerged aquatic plants (Weller 1975), although lack of food in marine bays and estuaries can force them to rely on salt marsh vegetation (R. Creedan, pers. comm.). In this paper we examine the spatial, temporal (time of day and year), tidal, and weather-related (wind, temperature, precipitation, cloud cover) factors influencing the abundance and local distribution of Brant and Canada Geese at Jamaica Bay Wildlife Refuge. The refuge on Long Island, New York is a 3600-ha coastal estuary containing a variety of tidal mudflats and marshes, and two large man-made freshwater ponds. This variety of habitats provides sufficient diversity for habitat selection. The results reported herein are part of an extensive study of how waterbirds use Jamaica Bay Wildlife Refuge, and results relating to other groups of birds are discussed elsewhere (Burger 1982, 1983a,b).

STUDY AREA AND METHODS

Jamaica Bay Refuge, part of the Gateway National Recreational Area (National Park Service), is located on the south shore of western Long Island, New York. The bay, a tidal lagoon containing many salt marsh islands, is shallow (less than 3 m deep at low tide) except for dredged channels. During late summer and fall the tidal fluctuation in Jamaica Bay averages 1.4 m (range = 0.9—2.13 m). The area of mudflats exposed at low tide varies with the lunar cycle and seasons. There are approximately 374 ha of low salt marsh (containing primarily cordgrass [Spartina alterniflora]) submerged at mean high tide, and exposed at mean low tide. High salt marsh (213 ha, mostly salt hay [S. patens]) occurs in well drained areas above the mean high tide limit.

Surrounded by the bay are two freshwater impoundments that were created by the deposition of spoil in 1953 (West Pond—17 ha, East Pond—39 ha). The National Park Service personnel lower the water levels in West Pond on 1 April (it gradually fills up by early summer) and they lower water levels in East Pond after 1 July each year. East Pond is completely surrounded by phragmites (Phragmites communis), although West Pond is bordered by this plant on only one side.
The refuge is bordered by J. F. Kennedy International Airport, residential communities, several active sanitary landfills, and expressways. Human disturbance is generally minimal in most areas of the bay (Burger 1981). A path around West Pond provides easy access, although joggers (present nearly daily in the summer) flushed the birds from the edge of the pond. Few people ever visited East Pond, and a trail had to be hacked through the phragmites to allow censusing.

For purposes of this study, Jamaica Bay Wildlife Refuge was divided into three census areas: tidal bay, East Pond, and West Pond. Brant and Canada Geese were censused during daylight from 31 May 1978–31 May 1979. The two ponds were censused 4 days per week every other week (8 h/day), and on two days on the alternating weeks. The ponds were censused twice daily (at low and high tide). Birds in West Pond were censused at prescribed stops (which allowed coverage of the entire pond), while those in East Pond were censused at stops determined by flock location. During each census the locations of all birds were plotted on maps of the ponds, and all areas of each pond were censused.

The tidal bay, visited 2 days every other week, was censused by following a route around its perimeter which included 17 stops where birds were counted. At each stop a census area was mapped. The 17 maps covered all visible areas of the bay with no overlap, although it was possible to see many areas from several census stops. On each census day, the locations of all birds were plotted on the 17 maps.

During each census we also recorded environmental variables, grouped into three categories: temporal, tidal, and weather. Temporal variables include date and time of day; tidal variables include tide cycle, tide direction, and tide height; and weather variables include wind velocity, wind direction, cloud cover, precipitation, and temperature. Although the tidal variables are all related (tide time, tide height), they generally were not highly correlated. Variables were defined and measured as follows: date—day of the year; time—time of the census on a 24 h clock; tide cycle—number of h before (−) or after (+) low tide; tide height—a relative value of the water level of the bays derived from tide tables; tide direction—rising (+) or falling (−) tide; wind direction—direction of the wind (N, NE, E, SE, W, NW); wind velocity—speed of wind recorded at Kennedy Airport on the edge of Jamaica Bay; cloud cover—estimated at each census location, recorded as a percent; precipitation—scored from 0 (none)–9 (heavy rain or snow); temperature—recorded from a hand carried thermometer and corrected against readings from Kennedy Airport.

Wind velocity was measured several times throughout each day, and the average wind-speed was used for analysis. For the purposes of presentation we divided wind velocity into categories. However, gusts of much higher velocity occurred in each category as follows: 0–3 mph (gusts up to 20), 3–6 (up to 40), >6 (over 40 gusts).

To assess the importance of these variables to our dependent measures (number of flocks, number of individuals) we used stepwise multiple regression procedures to determine the variables that should be entered in the model (including interactions [Barr et al. 1976]). Most independent variables were ordinal, and could be analyzed without transformations. Since wind direction was not ordinal, a new variable was created which compared the dependent measures at each wind direction against all other wind directions; examining each wind direction in turn. If any wind direction was significant it was entered into the model. The stepwise procedure first selects the variable that contributes the most to the coefficient of determination \( R^2 \) and then selects the second variable that gives the greatest increase in \( R^2 \). This procedure is continued until all variables that have not been included in the model are not statistically significant. Thus, if variables were highly correlated only one variable (the one giving the highest \( R^2 \)) would be added to the model. This model selection procedure determines the best model, gives \( R^2 \) values and levels of significance for the model, as well as giving the F values and levels of significance for each of the contributing variables. In this paper we present the best models for each dependent variable and levels of significance
for the independent variables. In general, the independent variable giving the highest $R^2$ has the lowest probability, and enters the model first. Thus, the relative value of the probability levels are indicative of the contribution made by each variable (i.e., a variable significant at $P \leq 0.0001$ generally contributes more to the observed variation in the dependent variable than one that is significant at $P \leq 0.01$). All statistical procedures were performed on log transformed data (log$_e(x + 1)$). On graphs we plot logs for the number of birds and number of flocks. We also used $\chi^2$ tests to distinguish differences among means of different samples.

For most analyses we grouped data by location since each area was sampled separately. For convenience we often present the data in graphs showing each location so that comparisons can be made.

RESULTS

During the study Brant accounted for 65% of the over 200,000+ Brant and Canada Geese observed at Jamaica Bay Wildlife Refuge (Table 1). Brant used primarily the tidal bay, whereas Canada Geese used mostly West Pond. Brant formed the largest flocks, and the largest flocks were on the tidal bay (Table 1).

Factors affecting the numbers of Canada Geese and Brant.—The model for number of flocks of Canada Geese accounted for between 37% and 78% of the variability by temporal (only on West Pond), and weather variables (all areas, Table 2). Weather-related variables that significantly influenced the number of flocks were wind velocity, wind direction, temperature, and cloud cover. The models for the number of individual Canada Geese explained between 54% and 76% of the variability by date (except on the bay) and weather variables such as wind velocity and direction (bay, West Pond), temperature (bay, East Pond) and cloud cover (bay, see Table 2). In summary, variations in number and distribution of Canada Geese were accounted for by temporal and weather-related, but not tidal variables.

---

**Table 1**

**Occurrence and Mean (± SD) Flock Size of Brant and Canada Geese at Jamaica Bay Wildlife Refuge**

<table>
<thead>
<tr>
<th></th>
<th>N (± SD)</th>
<th>Bay (± SD)</th>
<th>West Pond (± SD)</th>
<th>East Pond (± SD)</th>
</tr>
</thead>
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<td><strong>Brant</strong></td>
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<td></td>
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<td></td>
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<tr>
<td>— No. individuals</td>
<td>193,372</td>
<td>68%</td>
<td>39%</td>
<td>2%</td>
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<td>— flock size</td>
<td>162</td>
<td>1962 ± 132.1</td>
<td>92.1 ± 63.1</td>
<td>85.1 ± 46.1</td>
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<tr>
<td><strong>Canada Goose</strong></td>
<td>9038</td>
<td>11%</td>
<td>64%</td>
<td>25%</td>
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<tr>
<td>— flock size</td>
<td>138</td>
<td>49.6 ± 36.1</td>
<td>110.6 ± 52.1</td>
<td>19.2 ± 9.2</td>
</tr>
</tbody>
</table>

*°* Represent relative numbers, since any given flock might remain at Jamaica Bay Wildlife Refuge for several weeks in the winter.
### Table 2

**Environmental Variables Influencing the Number of Individuals and Flocks of Canada Geese on Jamaica Bay Wildlife Refuge**

<table>
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<th>Variables</th>
<th>Bay Flocks</th>
<th>Bay Individuals</th>
<th>East Pond Flocks</th>
<th>East Pond Individuals</th>
<th>West Pond Flocks</th>
<th>West Pond Individuals</th>
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<td></td>
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<tr>
<td>( R^2 )</td>
<td>10.87</td>
<td>72</td>
<td>65</td>
<td>54</td>
<td>37</td>
<td>56</td>
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<tr>
<td>( F )</td>
<td>0.0004</td>
<td>11.95</td>
<td>11.01</td>
<td>5.70</td>
<td>6.33</td>
<td>16.08</td>
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<td>( P )</td>
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<td>0.0001</td>
<td>0.0005</td>
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<td>0.02</td>
<td>0.05</td>
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The models for the number of flocks of Brant explained between 24% and 77% of the variability by day and time (West Pond only), tidal, and weather-related variables (all areas, Table 3). The weather-related variables which entered the models for the number of Brant flocks were wind velocity and direction (both ponds), temperature (bay, East Pond), and cloud cover (bay, East Pond). The model for variability in the number of individual Brant explained between 39% and 79% of the variation by temporal (not on the bay), tidal (bay, East Pond), and weather variables (all areas, Table 3). Wind direction and velocity (all areas), temperature (bay, West Pond), and cloud cover (bay, East Pond) significantly influenced distribution and abundance. Thus, for both species, numbers were influenced by temporal and weather-related variables, but only Brant were
### Table 3
Environmental Variables Influencing the Numbers of Individuals and Flocks of Brant on Jamaica Bay Wildlife Refuge

<table>
<thead>
<tr>
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<th>Bay Flocks</th>
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Tidally-influenced. The effect of each class of variables will be discussed separately.

Temporal variables.—The number of flocks of Brant and Canada Geese varied throughout the year with most flocks of Brant on West Pond; and most flocks of Canada Geese on both ponds (Fig. 1). Peak concentrations of Canada Geese occurred from October–April (Fig. 2). The seasonal pattern in the numbers of Canada Geese shows an increase in late June and July in addition to the winter increase in population levels (Fig. 2). This influx may represent post-breeding dispersal from nearby nesting areas such as Brigantine National Wildlife Refuge (New Jersey). Most Brant were at Jamaica Bay from October–December, although Brant did
Fig. 1. Seasonal distribution of flocks of Brant and Canada Geese on the three census areas of Jamaica Bay Wildlife Refuge.
Fig. 2. Number of Canada Geese on Jamaica Bay as a function of month. Solid circle = 1, solid star = 2, open star = 3, and square = 4 observations.
Number of Brant on the census areas as a function of month; symbols the same as Fig. 2.
Fig. 4. Number of Brant flocks in the three census areas as a function of tide cycle. 0 = low tide; symbols the same as Fig. 2.
Fig. 5. Number of Canada Geese flocks in the three census areas as a function of tide cycle. 0 = low tide; symbols the same as Fig. 2.
migrate through from March–May (Fig. 3). Generally the number of individual Brant per census (day) was less during spring migration.

*Tidal influences.*—Several tidal factors, such as tide cycle, tide height, and tide direction, could influence the abundance and local distribution of Brant and Canada Geese. Tidal factors influenced the number of flocks
Fig. 7. Number of Brant in the three census areas as a function of tide cycle. 0 = low tide; symbols the same as Fig. 2.
Fig. 8. Number of Canada Geese in the three census areas as a function of tide cycle. 0 = low tide; symbols the same as Fig. 2.
and individuals of Brant but not of Canada Geese (Tables 2 and 3). More flocks of Brant occurred on the bay on a falling tide and at low tide than on a rising tide, although the reverse pattern is evident for Canada Geese (Figs. 4–6). Most sightings of Canada Geese were on a rising tide on the bay and West Pond, and on a falling tide on East Pond (Fig. 6). Similarly, there were more Brant on the bay on a falling tide and at low tide than on a rising tide (Fig. 7) but tidel level apparently did not influence numbers of Canada Geese (Fig. 8). Tide height also affected Brant numbers. More Brant were present on the bay at low tide heights, and on the ponds at high tide heights.

In the above analysis we examined the effect of tidal factors within each census area (bay, East Pond, West Pond). Comparing the effect of tidal factors among census areas indicates significant differences in tide direction (but not tide cycle) for Brant, but not for Canada Geese (Fig. 6, Table 4). Brant used the bay and East Pond on rising tides, and used West Pond equally with respect to tides.

**Weather factors.**—Precipitation did not significantly affect the distribution or number for either species. Numbers of flocks and individuals of Canada Geese (all areas) and Brant (all areas except the number of flocks on the bay, refer to Tables 2 and 3) were affected by wind velocity and direction. Brant used the bay less on high winds (mean wind velocity of over 6 mph with gusts much higher) compared to other areas (Fig. 9).

### Table 4

**Comparison of the Number of Flocks of Brant and Canada Geese Using the Bay, East Pond, and West Pond**

<table>
<thead>
<tr>
<th></th>
<th>Canada Geese</th>
<th>Brant</th>
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<tr>
<td></td>
<td>$\chi^2$</td>
<td>df</td>
</tr>
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<td>N</td>
<td>138</td>
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<td>Tide cycle$^a$</td>
<td>1.52</td>
<td>4</td>
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<tr>
<td>Tide direction$^c$</td>
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<td>2</td>
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<tr>
<td>Wind direction$^d$</td>
<td>14.20</td>
<td>6</td>
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<tr>
<td>Wind velocity$^e$</td>
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<td>Temperature$^f$</td>
<td>48.6</td>
<td>8</td>
</tr>
<tr>
<td>Cloud conditions$^g$</td>
<td>5.85</td>
<td>4</td>
</tr>
</tbody>
</table>

$^a$ Tide cycle divided into 2–6 h before low, 2 h before to 2 h after low tide, and 2–6 h after low tide.

$^b$ NS = not significant.

$^c$ Rising and falling tide.

$^d$ Four directions: NNE, ESE, SSW, and WNW.

$^e$ Divided into 0–3 mph, 3–6 mph, and >6 mph wind velocities.

$^f$ Divided into 10°C temperature blocks.

$^g$ Divided into 0%, 2–99%, and 100% cloud cover.
Fig. 9. Percent of Brant and Canada Geese present as a function of wind velocity on each census area. Data given in mph (as recorded); wind velocity given as mean velocities, but gusts could be much higher.

Significant differences existed in the use of each census area as a function of wind direction (Table 4): (1) Brant used the bay more during NNE and WNW winds than they used the ponds, and they used the ponds more during ESE and SSW winds; (2) Canada Geese used the bay mostly during WNW winds, and used the ponds when winds were from other directions; and (3) Canada Geese used the bay more during WNW winds than did Brant (Fig. 10).
Since Canada Geese were present throughout the year, they encountered a wider range of temperatures than Brant (Table 5). Nonetheless, significant differences in habitat use occurred (Table 5). Brant used the bay more at lower temperatures than the ponds, and they used the two ponds similarly. Canada Geese used the bay at low temperatures, West Pond at intermediate temperatures, and East Pond at all temperatures including very high temperatures (Table 5).

Cloud cover influenced the numbers of flocks of Canada Geese on East Pond only, and of Brant on both ponds; and cloud cover influenced the number of Canada Geese on the bay, and the number of Brant on the bay and East Pond (Tables 2 and 3). For both species there were no differences
### Table 5
Percent of Brant and Canada Geese on Each Census Area as a Function of Temperature (°C)

<table>
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<tr>
<th></th>
<th>&lt;-4°</th>
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<th>+8°-+18°</th>
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<td>0</td>
<td>21</td>
<td>58</td>
<td>21</td>
<td>0</td>
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<td>3</td>
<td>20</td>
<td>58</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>Bay</td>
<td>2</td>
<td>46</td>
<td>40</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td><strong>Canada Geese</strong></td>
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<td></td>
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</tr>
<tr>
<td>East Pond</td>
<td>12</td>
<td>30</td>
<td>12</td>
<td>14</td>
<td>32</td>
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<tr>
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<td>5</td>
<td>78</td>
<td>12</td>
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</table>

in how they used the census areas as a function of cloud cover (Table 4). For both species there were fewer flocks in lower cloud cover.

**DISCUSSION**

*Habitat comparisons.*—In this study Brant primarily used the tidal bay, and Canada Geese were most abundant on freshwater West Pond. Brant were usually found in rafts on the water, whereas Canada Geese frequently fed on shore near West Pond. Other researchers (Weller 1975, Fredrickson and Drobney 1979) report a similar pattern of foraging behavior and locations for these species during migration. Stewart (1962) and Daiber (1977) also noted that Canada Geese fed primarily on coastal marshes and fresh estuarine bay marshes in Maryland and Delaware.

*Temporal effects.*—Canada Geese occurred in the refuge throughout the year, whereas Brant were migrants and winter residents. The influx of Canada Geese in June and July indicates that the refuge is used as a post-breeding staging area for young of the year and adults. Presumably the post-breeding birds mostly used the freshwater ponds since the increase in usage occurred there (Fig. 3). Although post-breeding birds primarily used West Pond, they did use East Pond in July and August. This difference in usage reflects management practices: during the entire year there are grassy areas around West Pond which are suitable for foraging and loafing. However, East Pond is bordered by phragmites and there are loafing areas for the Canada Geese only when refuge personnel lower the water levels (1 July).

Time of day rarely influenced numbers, but there tended to be more birds on ponds late in the day. The ponds were frequently used as loafing
and preening areas by flocks. In this study, tidal and weather factors (see below) were more important than time of day as contributors to the variability in numbers of flocks and of individuals. Waterfowl do show a diurnal pattern in that they usually feed by day and sleep at night (see Campbell 1978, Nilsson 1970, Dunthorne 1971).

*Tidal influences.*—Although use of tidal marshes and sloughs by waterfowl is frequently mentioned in the literature on geese on wintering grounds (Stewart 1962, Weller 1975, Daiber 1977, Fredrickson and Drobney 1979), there is little quantitative data examining the effects of tides on waterfowl. However, for Common Eiders (*Somateria mollissima*) tide has been considered the dominant factor influencing numbers and distribution (Gorman 1970, Pounder 1971, Milne 1974). Campbell (1978) found that tidal factors determined where the eiders concentrated to feed, and that the largest numbers concentrated in tidal areas when the tide was low.

In the present study Brant showed a strong response to tides, concentrating on the bay as the tide dropped and at low tide. Canada Geese were less influenced by tide levels. We attribute these differences to differences in foraging behavior: Brant feed on aquatic plants while Canada Geese feed on terrestrial plants (see Weller 1975). Presumably if Brant can feed optimally at low tide, they would begin to concentrate in foraging areas as the water levels drop. In contrast, Canada Geese feeding on land are independent of tide.

*Weather influences.*—Despite references to the effects of weather on waterfowl (Fredrickson and Drobney 1979), few quantitative data of its effects, except for temperature, are available. However, our study provided an opportunity to examine the effects of weather by comparing how Canada Geese and Brant used the different census areas.

Both Brant and Canada Geese used the ponds more than the bay when temperatures were high, and they used the bay more than the ponds when temperatures were low. Neither species used the ponds when they were partially or completely frozen, but instead concentrated elsewhere on the refuge where water remained open and food available.

Wind also influenced the distribution and abundance of birds. During strong winds Brant and Canada Geese usually remained on the lee side of salt marsh islands, or rafted behind tall phragmites. Canada Geese were absent from the bay in the highest winds, and remained in the ponds which were protected from winds by tall phragmites. Brant were also present on the ponds during very strong winds.

As cloud cover increased so did numbers of flocks and individuals of both species. We are unable to account for the significant relationship between the increase in geese numbers and cloud cover, unless reduced light concentrated birds as some sort of defensive response. Furthermore,
for Brant that feed in the water, foraging conditions might be better under cloudy skies where bright sunlight does not reflect from the water’s surface. Bovino and Burtt (1979) first suggested this explanation for decreased success under sunny skies for Great Blue Herons (Ardea herodias). The results of this study suggest that the effect of cloud cover on Canada Geese and Brant require further study.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This study indicates that spatial, temporal, tidal, and weather conditions all contributed to the variability in the abundance and local distribution of Canada Geese and Brant at an east coast estuary. Brant, but not Canada Geese were influenced by tidal factors, and they concentrated on the tidal bay on a falling tide, and at low tide. Brant used the tidal areas extensively, while Canada Geese primarily used the freshwater ponds. The increase in Canada Geese in late summer must represent post-breeding adults and young Canada Geese and these birds used only the ponds, moving into East Pond when the water levels were lowered by refuge personnel. Both species used the census areas differently under different environmental conditions. The availability of a wide diversity of habitats provided adequate areas for use under a variety of environmental conditions. The two species could minimize the effects of low temperatures and strong winds by shifting habitats. This study suggests that it may be important to maintain a diversity of habitats in any refuge to allow waterfowl to compensate for changes in weather. The man-made freshwater ponds were extensively used by Canada Geese, suggesting that the creation of similar freshwater ponds elsewhere on the east coast might aid this species.

SUMMARY

Numbers and movements of Brant (Branta bernicla) and Canada Geese (B. canadensis) were studied at Jamaica Bay Wildlife Refuge between 1 May 1978 and 1 May 1979. Jamaica Bay contains a variety of tidal habitats as well as two large freshwater ponds. Brant primarily used the tidal bay while Canada Geese were concentrated around freshwater ponds. Multiple regression analysis indicated that temporal and weather-related factors influenced the number of flocks and individuals of Canada Geese, while temporal, tidal and weather factors influenced Brant. The largest numbers of Brant and their flocks were present on the bay on falling tides and at low tides. The paper discusses the effect of temporal, tidal, and weather-related factors on the abundance and distribution of Brant and Canada Geese at Jamaica Bay Wildlife Refuge, and concludes that geese will use a diversity of habitats during different environmental conditions.

ACKNOWLEDGMENTS

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LITERATURE CITED


DEPT. BIOLOGICAL SCIENCES, RUTGERS UNIV., NEW BRUNSWICK, NEW JERSEY 08903 (JB AND WW); DEPT. STATISTICS AND N.J. AGRICULTURAL EXPERIMENT STATION, RUTGERS UNIV., NEW BRUNSWICK, NEW JERSEY 08903 (RT AND GR). ACCEPTED 1 NOV. 1982.
FEEDING HABITAT OF BLACK SKIMMERS
WINTERING ON THE FLORIDA GULF COAST

BARBARA B. BLACK AND LARRY D. HARRIS

The Rynchopidae are noted for their unique bill structure and feeding method; the elongated mandible is an adaptation for skimming across the water’s surface to catch fish and aquatic invertebrates. Although Zusi (1962) described in detail the morphological adaptations of the North American Black Skimmer (*Rynchops niger niger*) the species’ ecological adaptations are less well understood. Earlier investigators have described Black Skimmers feeding in shallow tidal streams and pools (Chapman 1908, Pettingill 1937, Tomkins 1951, Erwin 1977) where the surface of the water was smooth (Bent 1921, Zusi 1962) and prey was concentrated (Zusi 1962). These studies suggested that skimmers occupy a narrow feeding niche as later described by Erwin (1977); however, no attempt has been made either to characterize or quantify features of Black Skimmer feeding habitat. The objectives of this study were to delineate characteristics of Black Skimmer feeding habitat, and to monitor the prey resource and the diet of wintering Black Skimmers.

MATERIALS AND METHODS

The study site was located in the tidal flats surrounding Cedar Keys (29°08’30”N, 80°02’30”W), a system of keys on the west coast of peninsular Florida roughly midway between the Suwannee and Wacassassa rivers. Study areas (Fig. 1) of 6.0 ha each were separated by at least 100 m of land or 400 m of water.

During the fall of 1979 preliminary observations of area use were made in 16 areas. In each of two trials, 12 areas were monitored in 12 time segments from 1 h before to 2 h after low tide according to a randomized block design. In the first trial skimmers were rarely or never seen in the vicinity of four areas (G, H, I, J) so the areas were dropped from observation in the second trial. Four other areas (M, N, O, P) in the skimmers’ observed range were added. The measurement of area use was based on the product of a numerical response (number of birds) and a functional response (number of forages per focal bird) for all groups seen during standard 10-min observation periods. A “forage” was defined as a skimming effort in which the bird did not alter its wingbeat to change direction or lift itself from the surface of the water; the focal bird of a group was that individual whose forages were counted. The use of study areas by skimmers was analyzed using ANOVA and Duncan’s multiple range test on transformed forage data.

During the winter of 1979–80 we made observations to characterize preferred feeding habitat using 12 descriptive variables (Table 1), the less obvious of which are described below. The number of other feeders was the number of birds of other species feeding in an area. The locational variable (distance from loafing site) represented the distance from the center of a study area to the nearest loafing site used by skimmers. Since loafing areas are inundated at certain tidal stages, we considered only those available at the time of observation. The distance to the mainland was measured by 500 m increments from a fixed
reference point on the mainland to the feeding site. The six physiognomic variables were recorded as follows. The tidal stage was classified as 1 of 12 one-h increments beginning with the previous high tide. Water depth was measured with a water depth marker at the deepest non-canal location in each study area. Patchiness was designated by one of four classes ranging from 1 = minimal land-water interspersion to 4 = maximal land-water interspersion. Shelter by land was scored from 1–10 (each integer representing 50 m of land)
Table 1
Variables Recorded during 10-min Observation Periods

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<tr>
<td>Distance from loafing site</td>
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</tr>
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<td>Distance to mainland</td>
<td>(DTM)</td>
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<tr>
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 depending on the amount of land adjacent to an area in the direction of the prevailing wind during the observation. The percentages of open water and land (mudflat or sandbar) in an area were estimated from 25 point readings taken in a standard pattern with a cross-wire ocular scope (Winkworth and Goodall 1962) and converted to percentage values. Ten-min observation periods were assigned randomly to six used areas for 20 h in each of the 12 tidal stages. If no feeding was observed during an observation period, then the observer moved to the next designated area. If feeding was observed, then the observer remained in the area until no feeding had occurred for 10 min. In this way 89 skimmer-feeding observations were recorded with accompanying environmental measurements. A principal factor analysis (procedure FACTOR, Statistical Analysis Systems, Helwig and Council [1979]) was used to analyze these data.

To further study feeding areas, we noted the number of forages in two zones: “edge,” a 2-m zone to either side of a land-water interface and “open water,” a zone including all other water in the area. The relative abundance of these zones was estimated from point samples converted to percentage values. Skimmer use was compared to feeding zone availability using a Chi-square test for goodness-of-fit. The prey resource was sampled in four areas during peak feeding by skimmers, low to incoming tide (Black and Harris 1981), and adjacent to land-water interfaces. In each area eight seine hauls were made on each of 8 days for a total of 64 seine hauls per area. The number of prey sampled were compared between days (random variable) and between areas (fixed variable) using ANOVA. Additionally, the stom-
ach contents of 13 skimmers collected while feeding were analyzed to determine the frequencies of occurrence, relative weights, and relative volumes of prey species captured.

In the winter of 1980–81 we used the 12 descriptive variables to compare two highly-used and two unused feeding areas at Cedar Key. This completed the identification, delineation, and quantification of preferred feeding areas at Cedar Key. To test these results in an independent location, we selected an area 175 km to the northwest. At this second location, St. Vincent National Wildlife Refuge, Franklin Co., Florida, study sites were compared using selected variables based on the results of the Cedar Key study and were assigned to a "suitable" or "unsuitable" status (Fig. 2). Observations of skimmer use then were conducted to test the null hypothesis of equal use by feeding skimmers.

Fig. 2. Locations of the study areas at St. Vincent National Wildlife Refuge, Franklin Co., Florida. Areas V and X were presumed "suitable" and areas T and U were presumed "unsuitable."
Table 2
Average Number of Black Skimmer Forages in Study Areas during Two Trials as Shown by Duncan's Multiple Range Testa on Transformed Forage Datab

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<thead>
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<tr>
<td>C</td>
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<td>A</td>
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<tr>
<td>K</td>
<td>2.6</td>
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<td>L</td>
<td>2.5</td>
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<tr>
<td>E</td>
<td>1.8</td>
</tr>
<tr>
<td>B</td>
<td>1.7</td>
</tr>
<tr>
<td>G</td>
<td>1.4</td>
</tr>
<tr>
<td>F</td>
<td>1.2</td>
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<tr>
<td>D</td>
<td>1.0</td>
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<tr>
<td>H</td>
<td>1.0</td>
</tr>
<tr>
<td>I</td>
<td>1.0</td>
</tr>
<tr>
<td>J</td>
<td>1.0</td>
</tr>
</tbody>
</table>

a Means joined by a single line do not differ significantly (P > 0.05).
b Data were transformed using a square-root transformation of (a + 1).
c See Fig. 1 for location of areas.

RESULTS

Habitat characteristics.—In two trials Black Skimmers used some feeding areas more frequently \( F = 5.91, \text{df} = 11, P < 0.01 \) \( F = 2.44, \text{df} = 11, P < 0.01 \) than others and in both trials used areas A and C significantly more \( P < 0.05 \) than most other areas (Table 2). Skimmers fed intermittently in eight areas (B, E, F, G, K, L, M, P), but were not observed feeding in six other areas (D, O, H, N, J, I).

Within areas skimmers fed more often near certain topographic features. Of the total forages recorded in the winter of 1979–80 \( N = 5461 \) 71% were within 2 m of a land-water interface. Thus, skimmers foraged significantly more \( \chi^2 = 40.8, \text{df} = 1, P < 0.0001 \) along the water’s edge than in areas of open water.

Measurements of environmental variables recorded during skimmer feeding were used to identify the key factors of intermittently and frequently used habitat (Table 3). The first three factors accounted for 83% of the variation in the original data: factor 1, factor 2, and factor 3 accounted for 50%, 20%, and 13% of the variation, respectively. The four variables with high loadings on factor 1 describe the structure of skimmer feeding habitat. These variables were water depth, patchiness, amount of open water, and amount of land (mudflat and sandbar). Factor 2 was com-
prised of variables primarily associated with the location of the feeding area. These variables were distance from loafing site, distance to mainland, shelter by surrounding land, wind direction, and number of other feeders. Two variables, wind speed and distance to the mainland, had high loadings on factor 3 and were related to wind speed.

When highly-used and unused feeding areas at Cedar Key were compared, no significant differences were found for any climatic variables (wind speed, wind direction) or temporal variables (minutes to sunset, tidal stage) (Table 4). Significant differences did occur between area types for some social, locational, and physiognomic variables. Used areas were characterized by more feeding birds of other species, as well as proximity to loafing sites and the mainland. Used areas were also typified by shallower water with more shelter provided by surrounding land, less open water, more land-water interspersion, and more mudflat.

At St. Vincent National Wildlife Refuge variables important in the iden-
### Table 4

<table>
<thead>
<tr>
<th>Variable</th>
<th>Used habitat</th>
<th>Unused habitat</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temporal</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min to sunset(^a)</td>
<td>266.7 ± 26.8</td>
<td>321.8 ± 24.1</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind direction(^b)</td>
<td>240.1 ± 14.3</td>
<td>201.6 ± 16.0</td>
<td>NS</td>
</tr>
<tr>
<td>Wind speed(^a)</td>
<td>7.6 ± 0.7</td>
<td>6.6 ± 0.5</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Social</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of other feeders(^b)</td>
<td>18.7 ± 6.5</td>
<td>2.1 ± 0.3</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td><strong>Locational</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from loafing site(^b)</td>
<td>5.9 ± 0.5</td>
<td>13.4 ± 0.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance to the mainland(^b)</td>
<td>2.8 ± 0.2</td>
<td>3.5 ± 0.1</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td><strong>Physiognomic</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tidal stage(^a)</td>
<td>7.8 ± 0.1</td>
<td>7.8 ± 0.1</td>
<td>NS</td>
</tr>
<tr>
<td>Water depth(^b)</td>
<td>13.4 ± 1.1</td>
<td>31.9 ± 1.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Patchiness(^e)</td>
<td>4.0</td>
<td>2.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Shelter by land(^b)</td>
<td>5.8 ± 0.5</td>
<td>1.9 ± 0.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mudflat or land(^a)</td>
<td>43.8 ± 2.8</td>
<td>8.2 ± 1.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Open water(^a)</td>
<td>22.7 ± 2.6</td>
<td>62.2 ± 1.6</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

\(^a\) Student’s t-test (homogeneous variance).

\(^b\) Approximate t-test (heterogeneous variance) (Steel and Torrie 1960:81).

\(^e\) Wilcoxon’s rank sum test.

\(^c\) N equals the number of 10-min observations.

\(^d\) Median value replaces mean.

Identification of structure (water depth, patchiness, percentage of land, and percentage of open water) were the principal criteria for our selection of “suitable” and “unsuitable” sites. Selection based on the second factor, location, was more difficult since the only areas with structural features similar to the non-used areas of Cedar Key were located close to, rather than far from, the mainland and were more sheltered by land. The other locational variable associated with factor 2 (distance from loafing site) was, thus, the secondary basis for area selection. The third factor, wind speed, did not vary significantly between area types at Cedar Key or St. Vincent and was, therefore, not heavily considered in study area selection at St. Vincent.

When “suitable” and “unsuitable” areas at St. Vincent were compared, no significant differences (P > 0.05) were found in climatic variables (wind
**Table 5**

Means ± SE, and Results of Statistical Analyses Comparing Variables in Suitable and Unsuitable Feeding Habitat in the St. Vincent’s Area

<table>
<thead>
<tr>
<th>Variable</th>
<th>Suitable habitat</th>
<th>Unsuitable habitat</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temporal</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min to sunset*</td>
<td>293.6 ± 22.6</td>
<td>310.6 ± 20.8</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind direction*</td>
<td>104.1 ± 15.1</td>
<td>108.9 ± 17.5</td>
<td>NS</td>
</tr>
<tr>
<td>Wind speed*</td>
<td>8.2 ± 0.6</td>
<td>7.6 ± 0.5</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Social</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of other feeders(^b)</td>
<td>10.2 ± 1.3</td>
<td>2.7 ± 0.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Locational</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Distance from loafing site(^b)</td>
<td>4.1 ± 0.4</td>
<td>19.1 ± 0.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance to the mainland(^b)</td>
<td>1.4 ± 0.1</td>
<td>1.0 ± 0.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Physiognomic</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tidal stage*</td>
<td>7.7 ± 0.1</td>
<td>7.8 ± 0.1</td>
<td>NS</td>
</tr>
<tr>
<td>Water depth*</td>
<td>21.0 ± 2.2</td>
<td>43.6 ± 2.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Patchiness*</td>
<td>4.0</td>
<td>2.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Shelter by land(^b)</td>
<td>4.4 ± 0.4</td>
<td>7.2 ± 0.7</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Mudflat or land(^b)</td>
<td>33.6 ± 3.2</td>
<td>0.7 ± 0.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Open water(^b)</td>
<td>19.7 ± 2.0</td>
<td>65.9 ± 1.2</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

\(^a\) Student’s \( t \)-test (homogeneous variance).

\(^b\) Approximate \( t \)-test (heterogeneous variance) (Steel and Torrie 1960:81).

\(^c\) Wilcoxon’s rank sum test.

\(^d\) \( N \) equals the number of 10-min observations.

\(^e\) Median value replaces mean.

As expected, significant differences were found for all structural variables (water depth, patchiness, percentage of mudflat, percentage of open water) and the locational variable (distance from loafing site) by which the area types were selected. In addition, “suitable” areas had more feeders of other species, but were less sheltered by land and were farther from the mainland than “unsuitable” areas. Allowing for these two differences, the area types at Cedar Key and St. Vincent were similar for all other variables tested.

At St. Vincent, Black Skimmers used “suitable” areas 2.5 times more frequently (obs. = 105) than they used “unsuitable” areas (obs. = 39); thus, a significantly unequal distribution of forages (\( \chi^2 = 15.1, \ df = 1, \ P < 0.01 \)) was recorded in the two area types. These results indicate that feeding habitat selection of St. Vincent’s Black Skimmers was consistent...
Table 6
Means ± SE, and Results of Duncan’s Multiple Range Test for the Number of Fish and Shrimp per Seine Haul in Two Highly Used Areas (A and C) and Two Unused Areas (D and O) at Cedar Key

<table>
<thead>
<tr>
<th>Area</th>
<th>Preference class</th>
<th>Number of seine hauls</th>
<th>x ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>high</td>
<td>64</td>
<td>293.5 ± 44.2</td>
</tr>
<tr>
<td>D</td>
<td>non</td>
<td>64</td>
<td>195.2 ± 73.7</td>
</tr>
<tr>
<td>A</td>
<td>high</td>
<td>64</td>
<td>124.1 ± 38.6</td>
</tr>
<tr>
<td>O</td>
<td>non</td>
<td>64</td>
<td>66.4 ± 8.9</td>
</tr>
</tbody>
</table>

with that of Cedar Key Black Skimmers and predictable from the factor analysis of Cedar Key habitats.

Prey resource and diet.—At Cedar Key prey abundance did not differ significantly ($F = 0.82$, df = 7, $P > 0.5$) between days but did vary significantly ($F = 4.63$, df = 3, $P < 0.01$) between areas. Area differences, however, were not consistent with skimmer use since some highly used and unused areas did not differ significantly in prey numbers (Table 6). Prey levels were not necessarily higher in preferred feeding areas nor consistently lower in non-preferred areas. Additionally, prey composition was similar in all areas (Fig. 3); shrimp and members of the Sciaenidae (Perciformes) made up at least 87% of the total catch in each area.

From the skimmer stomachs examined, a total of 63 identifiable items were recovered of which 60% were shrimp and 40% were fish. However, fish were the predominant prey taken by both weight and volume (81% and 77%, respectively). In order of frequency the fishes recovered were: eight longnose killifish (*Fundulus similis*); seven striped mullet (*Mugil cephalus*); three Gulf killifish (*F. grandis*); two unidentified larvae (*Sciaenidae*); one diamond killifish (*Aedea xenica*); one Atlantic thread herring (*Opisthonema oglinum*); one tidewater silverside (*Menidia beryllina*); one needle nose fish (*Belonidae*); one unidentified larva (*Clupeiformes*). The three most frequently captured fish were also the largest types of prey being eaten.

Although shrimp were the most abundant prey recovered, they represented only 7% of the weight and 9% of the volume of the stomach contents examined. Shrimp species identified from whole specimens included: four *Palaemonetes pugio*; two *P. intermedius*; and one *P. vulgaris*. Finely digested material accounted for 12% of the weight and 14% of the volume of the stomach contents analyzed.
DISCUSSION

A premise underlying this study is that a species with stereotyped feeding behavior (Morse 1980) will be specific rather than plastic in feeding habitat choice. Erwin (1977) reported on the foraging zone use of three species of seabirds (Common Tern [Sterna hirundo], Royal Tern [Sterna maxima], and Black Skimmer) and found that skimmers were the most restricted in their habitat use. Among open bay, beach/inlet, tidal creek and marsh/tidal pool habitats, Erwin (1977) found that skimmers fed almost exclusively in marsh/tidal pools. In our study, which looked at feeding
only within the marsh/tidal-flat habitat, microhabitats were not used equally since skimmers fed in some areas frequently, in some intermittently, and in some not at all. Although some of the unused areas (J, I, H) were outside of the observed feeding range of the skimmers, other areas (D, N, O) were traversed frequently by foraging birds but were not used as feeding sites. Apparently, then, skimmers were selecting specific patches of habitat in which to feed within a single habitat type.

Skimmers should select feeding areas where they are either most successful or consistently successful in capturing prey. If one assumes that no other factor or factors affect skimmer feeding, then skimmers should feed most often in those areas of high prey abundance. However, this has been shown not to be the case since areas of high use and non-use did not differ significantly in prey abundance. In addition, prey composition was similar among all areas sampled and skimmer diets consisted of species of similar abundance in all areas. Other factors must, therefore, be involved in the selection of feeding areas.

The “structure” of feeding areas was found to account for the most variation in skimmer area use. Feeding areas were characterized by shallow water (10–20 cm), maximal land-water interspersion, and an average of 43% mudflat and 23% open water. These conditions typically occurred only in certain areas at or just after low tide (the skimmers’ primary foraging period) at Cedar Key (Black and Harris 1981). At low tide, unused areas typically had deeper water, less land-water interspersion, less mudflat, and more open water than highly used areas. In areas with deep water (>30 cm), 60% open water, and minimal land-water interspersion, edge zones created by land-water interfaces are reduced. Skimmers may not select these areas since they prefer to feed along edges. Because the skimmers’ feeding range is restricted to the top 5–6 cm of water, it is seemingly advantageous for skimmers to forage in shallow water, i.e., edge zones, where prey are concentrated vertically and/or escape downward is not possible. Of 5461 forages recorded, 71% occurred within 2 m of a land-water interface. Thus, skimmers fed more in the shallow water along land-water interface zones and areas with more land-water interface zones were preferred.

SUMMARY

The winter feeding ecology of Black Skimmers (Rynchops niger niger) was observed for 1119 h in 16 areas at Cedar Key and four areas at St. Vincent National Wildlife Refuge on the Gulf coast of Florida. Skimmers used some tidal flat areas frequently, some intermittently, and some not at all; however, prey abundance and composition alone did not explain the Black Skimmers’ selection of feeding areas. Of 5461 forages recorded, 71% occurred within 2 m of a land-water interface suggesting that the skimmer is best adapted to exploit prey in the shallow, smooth water along land-water interfaces. The structure of feeding areas
used by skimmers was typified by shallow water (10–20 cm), maximal land-water interspersion, 43% mudflat, and 23% open water. Feeding sites within marsh/tidal pool habitat were specifically selected by skimmers, and an assessment of specific habitat characteristics in two independent locations showed similar feeding habitat selection in two skimmer populations.

ACKNOWLEDGMENTS

We wish to thank R. Carter for statistical advice, C. R. Gilbert, J. Williams, and L. Bielsa for identifying fish and shrimp species and especially R. W. Gregory for assistance throughout the project. We are also grateful to M. Perry and the staff of St. Vincent National Wildlife Refuge for their cooperation and assistance, and to J. W. Hardy, R. M. Erwin, P. A. Buckley, and R. Zusi for reviewing and commenting on earlier drafts of the manuscript. This study was supported by the U.S. Fish and Wildlife Service, Contract No. 14-16-0009-79-063. The Florida Cooperative Fish and Wildlife Research Unit is supported jointly by the U.S. Fish and Wildlife Service, Florida Game and Fresh Water Fish Commission and the University of Florida.

LITERATURE CITED


CO-OPERATIVE FISH AND WILDLIFE RESEARCH UNIT, SCHOOL OF FOREST RESOURCES AND CONSERVATION, UNIV. FLORIDA, GAINESVILLE, FLORIDA 32611. ACCEPTED 15 NOV. 1982.
TROPHIC STRUCTURE OF BIRD COMMUNITIES IN FOREST PATCHES IN EAST-CENTRAL ILLINOIS

JOHN G. BLAKE

Consideration of the trophic structure of avian communities (e.g., Wilson 1974, Terborgh 1977, Faaborg 1982) provides information on community structure and organization that simple analyses of species richness, diversity, and density do not. Trophic structure reflects, at least in part, the importance of various food resources and variation in trophic structure may therefore reflect variation in availability of food resources among communities.

Trophic structure of avian communities has been studied by many researchers (e.g., Pearson 1975, Karr 1980, Landres and MacMahon 1980, Wagner 1981, Blake 1982), but only Martin (1980, 1981) has applied the concept to bird communities found in isolated patches of forest ("forest islands"). Instead, the relationship between area and species richness has been the focus of most forest island studies (e.g., Moore and Hooper 1975; Galli et al. 1976; Whitcomb et al. 1977, 1981). Forest islands differ in size and vegetation composition, factors that are likely to influence variety and quantity of food resources (Ghiselin 1977; Muhlenburg et al. 1977a, b; Jaenike 1978; Ranney et al. 1981). As a consequence, species richness and abundance of individuals within different trophic assemblages may differ in their relationship to forest size and structure (Martin 1980, 1981). Analysis of trophic structure and, in particular, how different groups vary in response to area, may provide a more complete understanding of the factors that govern overall community structure.

In the following discussion I examine the distribution of species and individuals among different trophic groups found in isolated patches of forest in east-central Illinois. Total species richness and abundance of individuals was strongly correlated with forest area, but the relationship differed among the various trophic groups. Ecological generalists were more abundant in small forests; many used habitat outside forest boundaries for foraging. More specialized species, including many foliage and bark gleaning insectivores, were poorly represented in small forests but were more abundant in large forests.

METHODS

I studied breeding bird communities in 15 forest tracts ranging in size from 1.8–600 ha in east-central Illinois. Thirteen tracts were censused in 1979, 14 in 1980, and six in 1981. All tracts possessed a mature canopy and well-developed understory, and did not show evidence of recent, heavy disturbance. With the exception of a minor amount of edge clearing that
occurred on several sites during winter 1979-80, forests were not disturbed during this study. Large tracts of forest (i.e., over 100 ha) are rare in east-central Illinois and are associated with rivers in almost all cases. As a consequence, both upland and bottomland forest occurred on some study areas.

Birds were surveyed using the point-count technique (Ferry and Frochot 1970, Robbins 1978). Within each forest, one or more study sites were established (hereafter, study area refers to an entire forest tract and study site to a specific census area within the forest). Forest tracts smaller than 20 ha contained a single study site; tracts larger than 20 ha were subdivided into two or more sites. Study sites were located in both edge and interior sections of large forests. Areas containing both bottomland and upland habitat had study sites in each. Within each study site, two or more observation points, ca. 150 m apart, were selected so that the entire study site was covered as thoroughly as possible.

Censuses were conducted from 30 min before sunrise to 2.5 h after sunrise, with two study sites surveyed each morning. Each observation point was visited for 15 min per census. Each 15-min period was divided into three 5-min segments, during each of which all birds seen, or heard were recorded. Birds flying above the canopy, raptors, and nocturnal species were not included. Singing males, family groups, and nests of all other species were counted as one pair; all other observations of single birds were counted as one-half pair. Scientific names of all species recorded are in the Appendix.

The point-count technique does not provide estimates of absolute density (pairs/ha) but it does provide data for comparison of relative levels of bird activity or abundance. Abundance for a study area or site was expressed as the sum of maximum recorded abundance of individual species at all points, divided by the number of points within the study area or site. The value for abundance thus gives average maximum number of individuals observed per point and allows comparison of observable levels of bird activity. Abundances of individual species were used to determine abundance within trophic groups.

Species were divided into trophic groups, including omnivore, granivore, ground, bark, foliage, and aerial insectivore, and nectarivore-frugivore. Classifications were based on primary food type and foraging location using personal observations and data from the literature (Martin et al. 1951, Willson 1974).

Area relationships were examined by linear regression using an exponential model: \( S = k \ln A + c \), where \( S \) is number of species or individuals within a trophic group, \( A \) is forest area (in ha), and \( k \) and \( c \) are fitted constants. I use the exponential model rather than the power function \( (\ln S = z \ln A + \ln c) \) because the former model explained a greater proportion of variance in community composition (Blake 1983). Species richness and abundances were tested for normality (Shapiro-Wilks test, Barr et al. 1979) and with one exception, no data sets showed a significant departure from normality. Distribution of aerial insectivore richness values was not normal \( (P < 0.05) \) and tests of significance were not applied.

As species richness increases, the number of species within trophic groups is expected to increase simply as a function of species richness. Therefore, I compared the observed distribution of species within trophic groups to the distribution expected by chance. I generated a series of randomly assembled sets of species, using the total pool of species recorded from forest islands. For each species richness value (5, 10, 15, . . . , 40), 10 sets of species were drawn with no species included more than once in a single draw. Distribution of species among trophic groups within these randomly assembled communities was then compared to observed distributions (binomial probability test, Sokal and Rohlf 1981).

RESULTS

Species richness within trophic groups.—Only nectarivore-frugivore (two species) and granivore (two species) groups contained fewer than three
species. Neither group was represented by many individuals in any year and I have focused attention on the number of species and individuals within the remaining five groups (Table 1).

All five major trophic groups were represented by at least one species on all study areas in 1979 but not in 1980 or 1981, when foliage insectivores were absent from the smallest tract. Dominant groups (i.e., those represented by the most species or individuals) varied among areas. Omnivores were dominant on all areas less than 28 ha in 1979. However, because the number of omnivores did not vary greatly among areas (5–8 species, Table 1), percentage representation of this group decreased with area (Fig. 1). By contrast, both foliage and bark insectivores increased in species richness with area, with the increase especially great for foliage insectivores (Fig. 1). Thus, as forest size increased, community composition changed from omnivore dominated to foliage insectivore dominated in 1979.

More omnivores were recorded in 1980 than in 1979, but numbers of species in all other groups remained unchanged (Table 1). As a consequence, there was not a clear change in 1980 from omnivore dominated to foliage insectivore dominated communities as area increased (Fig. 1).

### Table 1

<table>
<thead>
<tr>
<th>Area</th>
<th>Size (ha)</th>
<th>Omnivores</th>
<th>Bark insects</th>
<th>Ground insects</th>
<th>Foliage insects</th>
<th>Aerial insects</th>
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<tbody>
<tr>
<td></td>
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<td>SP</td>
<td>IND</td>
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<td>7.0</td>
<td>8.0</td>
<td>4.3</td>
<td>2.6</td>
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<tr>
<td>10</td>
<td>28</td>
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<td>8.4</td>
<td>7.3</td>
<td>6.1</td>
<td>4.7</td>
</tr>
<tr>
<td>11a,b</td>
<td>40</td>
<td>8.0</td>
<td>12.8</td>
<td>6.0</td>
<td>7.4</td>
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<td>14</td>
<td>118</td>
<td>7.5</td>
<td>6.2</td>
<td>6.5</td>
<td>4.6</td>
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<tr>
<td>15</td>
<td>600</td>
<td>8.7</td>
<td>8.3</td>
<td>8.0</td>
<td>6.4</td>
<td>6.0</td>
</tr>
</tbody>
</table>

* Censused only in 1 year; not included in regression analyses (Table 2).
* Bottomland forest habitat only.
However, percentage representation by omnivores was still highest at the smallest area and lowest at the largest forest (Fig. 1).

Patterns in 1981 were most similar to 1979. (Only six areas were censused and results are not shown graphically.) Fewer foliage insectivores were recorded, but larger areas were still dominated by this group.

Species richness within the five major trophic groups was significantly correlated with area in all years (Table 2). Foliage insectivores are predominantly long-distance migrants, many of which prefer large forest tracts for breeding (Whitcomb et al. 1981) and species richness within this group increased strongly with area. The rate of increase (slope) in bark insectivore richness with area also was high (Table 2). The importance of area for these two groups was further demonstrated by intercept values that did not differ from zero (Table 2), indicating that very small patches of forest were unsuitable for members of these groups. By contrast, ground insectivores, which also were strongly correlated with area, had a higher intercept, indicating that a number of species were not restricted by area
Table 2
Relationship Between Area (ln) and Number of Species and Individuals (Pairs/Point) in Major Trophic Groups; Results Averaged over 3 Years, 1979-1981; Only Areas Censused in 2 or 3 Years are Included (n = 12)

<table>
<thead>
<tr>
<th>Trophic group</th>
<th>Slope</th>
<th>Intercept</th>
<th>R</th>
<th>P&lt;</th>
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<tr>
<td>Species richness</td>
<td></td>
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<td></td>
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<tr>
<td>Omnivores</td>
<td>0.65</td>
<td>5.0</td>
<td>0.875</td>
<td>0.001</td>
</tr>
<tr>
<td>Bark insectivores</td>
<td>1.29</td>
<td>0.7</td>
<td>0.917</td>
<td>0.001</td>
</tr>
<tr>
<td>Ground insectivores</td>
<td>0.79</td>
<td>1.5</td>
<td>0.933</td>
<td>0.001</td>
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<tr>
<td>Foliage insectivores</td>
<td>1.87</td>
<td>-0.1</td>
<td>0.962</td>
<td>0.001</td>
</tr>
<tr>
<td>Aerial insectivoresa</td>
<td>0.32</td>
<td>1.4</td>
<td>0.913</td>
<td>—</td>
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<table>
<thead>
<tr>
<th>Abundance of individuals</th>
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<tr>
<td>Omnivores</td>
<td>-0.20</td>
<td>8.5</td>
<td>-0.250</td>
<td>NS</td>
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<tr>
<td>Bark insectivores</td>
<td>1.10</td>
<td>0.1</td>
<td>0.856</td>
<td>0.001</td>
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<tr>
<td>Ground insectivoresb</td>
<td>0.52</td>
<td>2.3</td>
<td>0.582</td>
<td>0.05</td>
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<tr>
<td>Foliage insectivores</td>
<td>0.94</td>
<td>1.7</td>
<td>0.868</td>
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<tr>
<td>Aerial insectivores</td>
<td>0.21</td>
<td>2.1</td>
<td>0.647</td>
<td>0.05</td>
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</table>

a Distribution of values not normal, significance value omitted.
b Ground insectivore abundance was not correlated with area in any one year.

of forest habitat. Flycatching or aerial insectivores were few in number and showed little increase in species richness with area (Table 2). Omnivores displayed the weakest correlation with area and had the highest intercept in all years. The high intercept reflects dominance of omnivores in small forests and also indicates that many species were not restricted to large tracts of forest.

Increased species richness within larger forests is at least partially due to spatial segregation of species; not all species occur within the same section (study site) of a forest that occur within the entire forest (study area). Data from study sites partially reflect spatial segregation of species and can be used to compare species richness within subsections of a series of forests as total forest area increases. In this study, patterns observed among study areas generally held among study sites, although correlations and slopes generally were lower. The relationship between aerial insectivores and area differed least between study areas and sites. Bark and foliage insectivores remained strongly correlated with area, but with reduced rates of increase. Species richness in omnivore and ground insectivore groups was not correlated with area among study sites.

As species richness in forests increases, species richness within major trophic groups also should increase. I compared observed species richness in trophic groups to that expected from randomly assembled species groups.
Fig. 2. Species richness of major trophic groups plotted as a function of total species richness. Dashed lines represent the relationship between total species richness and species richness in major trophic groups within randomly generated communities. 1979—closed circles; 1980—x's; and 1981—open circles. O = omnivores; Bl, Gl, and Fl = bark, ground, and foliage insectivores, respectively.

(Aerial insectivores were not considered in this fashion because of low species richness.) Previous studies from New Jersey (Galli et al. 1976) and Illinois (Blake 1983) have indicated that the rate of increase in species richness with area begins to level off at approximately 20–24 ha. In Illinois forests, areas smaller than 20 ha ranged from 2–16 ha and, with one exception (area 3, 4.7 ha), supported fewer than 20 species. Forests $>20$ ha ranged from 24–600 ha and all supported more than 20 species. (Area 3 was connected by a hedgerow to a larger forest and had a higher than
expected species total [Blake 1983].) I divided forests into those with fewer than 20 species and those with more than 20 species. I then compared distribution of points above and below the regression line for random assemblages for all forests and, separately, for forests with less than and more than 20 species, “small” and “large” forests, respectively.

Omnivores were, overall, more common than expected over the entire range of areas \((P < 0.02)\) (Fig. 2). However, when small and large forests were examined separately, omnivore richness was higher than expected in small tracts \((P < 0.003)\) but not in large tracts \((P = 0.14)\). Apparently, many omnivores are attracted to small forests, perhaps as a consequence of the greater proportion of available edge habitat and the accessibility of surrounding habitat for additional foraging.

More bark insectivore species were present than expected \((P < 0.04)\) over the entire range of islands and in large forests \((P < 0.003)\), but not in small forests \((P = 0.12)\). Ground insectivores were more common than expected over all size classes \((P < 0.001)\), in large forests \((P < 0.03)\), and non-significantly \((P < 0.10)\) in small forests (Fig. 2). Foliage insectivores displayed the greatest deviation from expected. In no case was observed species richness greater than expected based on random assemblages \((P < 0.001)\) (Fig. 2).

Distribution of species richness patterns in trophic groups is not independent because the total species pool was divided into relatively few groups. Thus, if one group appears under-represented at one area, some other group(s) must be over-represented. However, the consistency of the patterns argues for their validity. Trophic groups are not represented in all islands simply according to their contribution to the total species pool.

**Abundance of individuals within trophic groups.**—Based on abundance of individuals, larger areas were not dominated by foliage insectivores to the same extent that they were when species richness was considered (Table 1, Fig. 1). Omnivores showed a slight tendency to decrease in total numbers with increasing area, but the decline was not great. Omnivores not only remained numerically dominant on smaller areas (Table 1), but also were usually the most abundant group on all areas. Percentage representation declined as area increased (Fig. 1), due to increases in other trophic groups.

Correlations between area and abundance within trophic groups generally were not as high as correlations between area and species richness (Table 2). Bark and foliage insectivores were most strongly correlated with area; intercepts were low and not different from zero. The rate of increase (slope) in abundance was approximately the same for both groups. As area increased, bark insectivores added individuals at approximately the same rate as species, but this was not true for foliage insectivores. As a result,
average abundance per species within the latter group decreased ($P < 0.05$) with increasing area. Of the remaining groups, only aerial insectivores were significantly associated with area in a single year and only in 1979. As a consequence, increased abundance in forests was primarily due to increased numbers of bark and foliage insectivores with some increase in aerial insectivore abundance. With all years combined, ground insectivore abundance was significantly correlated ($P < 0.05$) with area (Table 2), but correlation with area was not significant in any single year.

Patterns generally were similar among study sites. Aerial insectivore abundance was significantly correlated with area in 1979 and 1980. Unlike species richness, rates of increase in abundance within trophic groups were not generally less among study sites when compared to study areas.

**DISCUSSION**

Bird communities within small patches of forest are not random subsets of all species that commonly breed in forests (Galli et al. 1976, Whitcomb et al. 1981); many species are restricted to forests that exceed some minimum area requirement. The influence of area on patterns of species distribution also is apparent when bird communities are examined from a trophic standpoint.

Small patches of forest consist largely of edge habitat (Forman and Godron 1981) and are dominated by birds that feed on a wide variety of food items both within the forest and in surrounding fields (Galli et al. 1976, Martin 1981, Whitcomb et al. 1981), illustrating a major difference between habitat islands and oceanic islands. Many omnivores and ground insectivores are short-distance migrants that winter north of the tropics. Many do not require large tracts of forest for breeding and many species present in small forest tracts are more typically found in thickets and second growth. Such species may occur in small forests because of their ability to forage outside actual forest boundaries. As a consequence, habitat surrounding forest islands may have a strong impact on the distribution and abundance of species and guilds within the island.

Forest edges may support a greater diversity and abundance of food than does forest interior habitat because of their high levels of productivity (Ranney et al. 1981). Species that prefer edge habitat do better in such areas than species more restricted in foraging behavior. In addition, species that are unable to supplement their diet by foraging in surrounding habitat may be influenced to a greater extent by competition or resource limitation. This may be particularly true if the more adaptable species are numerous enough to cause local resource depletion.

Species that glean insects from foliage generally were restricted in distribution among forests. Over the entire range of areas censused, foliage
insectivores were less common than expected, suggesting that some factor(s) limited occurrence of some species. Many foliage insectivores were long-distance migrants that winter in Central and South America. Neotropical migrants, as a group, have been most severely affected by forest reduction and fragmentation (Lynch and Whitcomb 1978, Keast and Morton 1980, Whitcomb et al. 1981). The apparently greater susceptibility of Neotropical migrants to population reduction following forest loss may be a consequence of several life history traits typically associated with long-distance migration (Whitcomb et al. 1981). For example, Neotropical migrants frequently construct open nests in low vegetation or on the ground and such nest-sites may be particularly susceptible to predation (Best 1978, Gates and Gysel 1978, Willis and Eisenmann 1979, Loiselle and Hoppes 1983) or parasitism by the Brown-headed Cowbird (Mayfield 1977, Payne 1977, Gates and Gysel 1978).

Low species richness in small forests may be a consequence, at least partially, of higher predation or parasitism rates (Lynch and Whitcomb 1978, Robbins 1979, Whitcomb et al. 1981) than those characteristic of large forests. If species characteristic of different trophic groups differed in overall susceptibility to predation, then observed differences in distribution patterns among trophic groups might be related to differences in predation and parasitism. Many foliage insectivores are Neotropical migrants that build open cup nests and the apparent paucity of foliage insectivores in small forests may therefore reflect high predation pressures. However, most omnivores, including both long-distance and short-distance migrants, also nest close to the ground in open cut nests and are not scarce in small forest tracts. Further, all bark insectivores nest in tree cavities (or beneath bark, Brown Creeper) well above the ground. However, bark insectivores were not abundant in small forests. (The scarcity of cavity nesters may be due to a shortage of available nest-sites [e.g., von Haartman 1956], but insufficient data are available to examine the possibility.) Increased nest predation and parasitism may influence bird communities in small forests, but it is not immediately apparent that trophic groups should be differentially affected.

Abundance and diversity of food resources also may influence distribution of species and individuals. There is some evidence that diversity and abundance of insects may be related to area (Muhlenberg et al. 1977a, b; Faeth and Kane 1978; Jaenike 1978) and it is possible that resource limitation may be partially responsible for the scarcity of foliage insectivores in small forests. Because most foliage insectivores largely depend on resources available within forest boundaries, the potential for resource limitation may be greater than for species that frequently forage in non-forest habitat (e.g., many ground insectivores, omnivores). If resources
are scarce, competitive interactions among foliage insectivores may influence observed distribution patterns. Previous studies have indicated that competitive interactions, both intra- and inter-specific, may be important among foliage insectivores (e.g., Morse 1967, 1970, 1974; Cody and Walter 1976; Catchpole 1978; Robinson 1981).

Bark insectivores were present over the entire range of areas censused; both Red-headed and Downy woodpeckers were recorded from the smallest area in 2 of the 3 years censused. The Red-headed Woodpecker uses a wider variety of food and foraging behaviors than other bark insectivores, frequently feeding on the ground in surrounding fields (pers. obs.). Greater plasticity in behavior may partially account for its occurrence in small forests. By contrast, Red-bellied Woodpeckers and especially Hairy Woodpeckers generally were confined to larger forests. Although large territory requirements (Graber et al. 1977) were likely partially responsible for the distribution patterns, competitive interactions, primarily with the Red-headed Woodpecker (Graber et al. 1977; Williams and Batzli 1979a, b), also may have influenced occurrence of Red-bellied and Hairy woodpeckers and other bark gleaners (e.g., White-breasted Nuthatch). The Hairy Woodpecker is generally uncommon in east-central Illinois and its numbers have been declining over the past decades (Graber et al. 1977). The decline may be related to concurrent losses of forest cover and increased isolation of remaining tracts of woods.

Previous studies of bird communities in relatively large habitat islands (Galli et al. [1976]—New Jersey; Whitcomb et al. [1981]—Maryland) have not dealt with trophic structure in any detail. Although similarities exist, important differences also are apparent. In all three regions, foliage and bark insectivores were most abundant in large forests and showed the greatest change in species richness from small to large forests. In addition, omnivores were the most abundant group in small forests and declined in relative importance as forest size increased. Abundance of omnivores in small forests may reflect the disturbed nature of such forests and parallels trends in fish communities, where disturbed habitats also are characterized by an increased abundance of omnivorous species (Karr 1981, Schlosser 1982).

Small (under 20 ha) Illinois forests supported few foliage insectivores or bark insectivores. By contrast, small forests in New Jersey and Maryland had approximately twice as many species in each trophic group. Species richness in other trophic groups did not differ as much among the three areas. Forests in the eastern states are less isolated than forests in Illinois and more non-agricultural habitat is available around and between forest patches. As a consequence, some species may be able to incorporate habitat adjoining forest patches in their foraging area. Resource levels
(e.g., insect abundance and diversity) within and immediately adjacent to forest patches also may be influenced by differences in farming practices between Illinois and more eastern states with consequent impacts on bird community structure.

Trophic composition of an island community may be influenced by a variety of factors, but an underlying factor is distribution, variety, and abundance of food resources. Islands that do not differ in structural and habitat features may support a similar resource base with similar consequences on consumer distribution and abundance. Habitat islands such as forest patches are not self-contained units to the same extent that true oceanic islands are. Biotic exchanges between the habitat patch and the surrounding matrix may have a large impact on the community associated with the island or refuge (Kushlan 1979, Forman and Godron 1981). The composition and structure of surrounding landscape can influence the community structure, including trophic structure, of habitat islands to a greater extent than is true for real islands. Thus, analyses of habitat island communities should include consideration of regional patterns of habitat structure.

SUMMARY

Trophic structure of breeding bird communities in isolated forests (1.8–600 ha) in east-central Illinois was studied 1979–1981. Breeding species were assigned to one of seven trophic groups: two groups (nectarivore-frugivore, granivore) were represented by few species or individuals. Abundance and species richness within the remaining five groups varied with forest area and appeared tied to the size and structure of the forest itself and to the composition of the surrounding landscape.

Small forests were dominated by omnivores that frequently foraged in surrounding farmland. Foliage insectivores, primarily Neotropical migrants, were uncommon in smaller forests, but comprised the largest component of bird communities in large forests. Species totals in major trophic groups were significantly correlated with area in all years. Highest correlations were observed for foliage insectivores and bark insectivores. The former group had the highest slope, indicating the most rapid increase in species number with area, a reflection of the increase in number of long-distance migrants in larger forests. Correlation with area generally was not as high for abundance of individuals within trophic groups. However, abundances of both foliage and bark insectivores were strongly correlated with area.

Over the size range of forests covered, distribution of species within major trophic groups differed from that expected if species occurrences were independent of forest area. Omnivores were more common that expected in small forests, whereas ground insectivores and bark insectivores were more common than expected in large forests. Foliage insectivores were underrepresented over the entire range of forest size. Thus, trophic groups were not represented in all forests simply according to their contribution to the total species pool, suggesting that abundance of different food resources varied in dissimilar ways with forest area.
ACKNOWLEDGMENTS

The present manuscript has benefitted from suggestions by J. C. Barlow, G. O. Batzli, W. G. Hoppes, J. R. Karr, B. A. Loiselle, M. R. Lynch, B. A. Mauer, G. D. Schnell, and M. F. Wilsson. B. A. Loiselle and J. R. Karr, in particular, have provided support and encouragement throughout this project and their efforts are greatly appreciated. This study was funded by the U.S. Fish and Wildlife Service, Contract No. 14-16-0009-79-23 to J. R. Karr.

LITERATURE CITED


Blake • COMMUNITY TROPHIC STRUCTURE


606 E. HEALEY ST., VIVARIUM BLDG., UNIV. ILLINOIS, CHAMPAIGN, ILLINOIS 61820. ACCEPTED 26 JAN. 1983.

APPENDIX

BIRD SPECIES RECORDED FROM FOREST TRACTS IN EAST-CENTRAL ILLINOIS DURING BREEDING SEASONS, 1979–1981

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic group</th>
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<tbody>
<tr>
<td>Mourning Dove (Zenaida macroura)</td>
<td>G</td>
</tr>
<tr>
<td>Yellow-billed Cuckoo (Coccyzus americanus)</td>
<td>Fl</td>
</tr>
<tr>
<td>Black-billed Cuckoo (C. erythropthalmus)</td>
<td>Fl</td>
</tr>
<tr>
<td>Ruby-throated Hummingbird (Archilochus colubris)</td>
<td>N-F</td>
</tr>
<tr>
<td>Northern Flicker (Colaptes auratus)</td>
<td>G1</td>
</tr>
<tr>
<td>Red-bellied Woodpecker (Melanerpes carolinus)</td>
<td>BI</td>
</tr>
<tr>
<td>Red-headed Woodpecker (M. erythrocephalus)</td>
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</tr>
<tr>
<td>Hairy Woodpecker (Picoides villosus)</td>
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</tr>
<tr>
<td>Downy Woodpecker (P. pubescens)</td>
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</tr>
<tr>
<td>Great Crested Flycatcher (Myiarchus crinitus)</td>
<td>Al</td>
</tr>
<tr>
<td>Acadian Flycatcher (Empidonax virescens)</td>
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</tr>
<tr>
<td>Eastern Wood-Pewee (Contopus virens)</td>
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</tr>
<tr>
<td>Blue Jay (Cyanocitta cristata)</td>
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<td>Black-capped Chickadee (Parus atricapillus)</td>
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<tr>
<td>Tufted Titmouse (P. bicolor)</td>
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</tr>
<tr>
<td>White-breasted Nuthatch (Sitta carolinensis)</td>
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Appendix
Continued

<table>
<thead>
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<th>Species</th>
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<tbody>
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<td>Brown Creeper (Certhia americana)</td>
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<td>House Wren (Troglodytes aedon)</td>
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<td>Gray Catbird (Dumetella carolinensis)</td>
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</tr>
<tr>
<td>Brown Thrasher (Toxostoma rufum)</td>
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<tr>
<td>American Robin (Turdus migratorius)</td>
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</tr>
<tr>
<td>Wood Thrush (Hylocichla mustelina)</td>
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<tr>
<td>Veery (Catharus fuscens)</td>
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<tr>
<td>Blue-gray Gnatcatcher (Polioptila caerulea)</td>
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<tr>
<td>Cedar Waxwing (Bombycilla cedrorum)</td>
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</tr>
<tr>
<td>European Starling (Sturnus vulgaris)</td>
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</tr>
<tr>
<td>Yellow-throated Vireo (Vireo flavifrons)</td>
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<tr>
<td>Red-eyed Vireo (V. olivaceus)</td>
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<td>White-eyed Vireo (V. griseus)</td>
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<td>Kentucky Warbler (Oporornis formosus)</td>
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<td>House Sparrow (Passer domesticus)</td>
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<tr>
<td>Red-winged Blackbird (Agelaius phoeniceus)</td>
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<tr>
<td>Common Grackle (Quiscalus quiscula)</td>
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<tr>
<td>Brown-headed Cowbird (Molothrus ater)</td>
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</tr>
<tr>
<td>Scarlet Tanager (Piranga olivacea)</td>
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<tr>
<td>Northern Cardinal (Cardinalis cardinalis)</td>
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</tr>
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<td>Rose-breasted Grosbeak (Pheucticus ludovicianus)</td>
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<tr>
<td>Indigo Bunting (Passerina cyanea)</td>
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<tr>
<td>American Goldfinch (Carduelis tristis)</td>
<td>G</td>
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<tr>
<td>Rufous-sided Towhee (Pipilo erythrophthalmus)</td>
<td>O</td>
</tr>
<tr>
<td>Chipping Sparrow (Spizella passerina)</td>
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</tr>
<tr>
<td>Field Sparrow (S. pusilla)</td>
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</tr>
<tr>
<td>Song Sparrow (Melospiza melodia)</td>
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</tr>
</tbody>
</table>

*Trophic groups are omnivore (O), granivore (G), ground, bark, foliage, and aerial insectivore (GI, Bl, Fl, and Al), and nectarivore-frugivore (N-F).*
THE IMPACT OF COTTAGE DEVELOPMENT ON COMMON LOON REPRODUCTIVE SUCCESS IN CENTRAL ONTARIO

MARIANNE HEIMBERGER, DAVID EULER, AND JACK BARR

In recent years, the increasing popularity of wilderness vacations has caused a sharp rise in recreational activity in many northern areas. In the Boundary Waters Canoe Area of Minnesota, for example, increased motorboat and canoe traffic appears to have a negative impact on the productivity of the Common Loon (Gavia immer); (Lucas 1967, Titus and Van Druff 1981). Lehtonen (1970) attributed a decline in the Arctic Loon (G. arctica) on Finnish lakes to increasing numbers of cottages and, in a 1-year study of 19 Alberta lakes, Vermeer (1973) found a significant, inverse correlation between the numbers of breeding Common Loons and the amount of human disturbance. Bundy (1979) and Andersson et al. (1980) also related that recreation appeared to have negative impacts on loons in Scotland and Sweden. The purpose of our study was to investigate the impact of cottage development on the reproductive success of Common Loons in central Ontario.

The Muskoka and Haliburton districts of central Ontario (Fig. 1) are favorite resort locations. Summer cottages are built along lakeshores and boating, swimming, fishing or other similar activities are common and often very intense for short periods, e.g., holiday weekends. Since loons must nest near the shoreline of small islands and bog hummocks, and young loons spend their time prior to fledging entirely on the water, extensive water-oriented recreation may be detrimental to loon productivity.

METHODS

Lakes selected for study were 31–190 ha in size and were similar in all respects except in intensity of cottage development, which ranged from totally undeveloped to a maximum of more than 10 cottages/500 m. Each lake had at least one Common Loon territory which included open water, free of emergent vegetation, sufficient room for display activity, a boating area, and adequate food for a pair of adult loons with chicks. A bog or small island was considered essential for nesting.

All islands, bogs and mainland shore areas with bog fringes were surveyed once every 2 weeks as soon as the ice was off the lakes until most chicks had fledged. Thirty-four lakes were surveyed in 1977. In 1978 and 1979, one lake was eliminated, and seven added for a total of 40 lakes which contained 50 potential Common Loon territories (Table 1).

Nest locations and clutch-sizes were recorded. The date on which incubation was initiated was estimated by subtracting 29 days (Olson and Marshall 1952) from the date of hatching. When eggs failed to hatch, only the date on which the nest was found was recorded. The number of hatched eggs was calculated by counting chicks and/or shell membranes. When
the chicks were first seen their age was determined by size and color of their plumage (Olson and Marshall 1952), a method accurate to within 3 days, and hatch date estimated.

The number of areas on the lakes which contained conditions judged suitable for a loon nest was recorded. These were islands and bog areas with characteristics known to be important to loons (Bent 1919, Olson and Marshall 1952, McIntyre and Mathisen 1977). These are areas close to the water, often in bogs or marshes, with gentle inclines to permit the birds to move to and from the nest with ease.

The distance from the nest to the nearest cottage and the number of cottages within 150 m of the nest was recorded and in 1979, human activity around 16 nests was also investigated. Eight of these nests had no cottages within 250 m and eight were within 150 m of a minimum of three cottages. Each nest was monitored on 4 rainless, weekend days during one of four time periods (07:00–08:30, 10:00–11:30, 13:00–14:30, 16:00–17:30) during incubation. The type and location of all human activity observed within 500 m of the nest was recorded on a grid map once every 5 min for each time period. Human activity occurring within 150 m of a nest was closely examined because it was assumed that activity close to the nest would have a greater detrimental effect on loon reproduction than that further away. For each nest,
Table 1

Summary of Common Loon Reproductive Success in Ontario 1977–1979

<table>
<thead>
<tr>
<th></th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of potential loon territories</td>
<td>44</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>No. of potential territories occupied</td>
<td>29</td>
<td>38</td>
<td>35</td>
</tr>
<tr>
<td>No. of territories with at least one nesting attempt</td>
<td>24</td>
<td>33</td>
<td>35</td>
</tr>
<tr>
<td>% potential territories with at least one nesting attempt</td>
<td>55</td>
<td>60</td>
<td>58</td>
</tr>
<tr>
<td>No. of territories with at least one egg hatching</td>
<td>17</td>
<td>23</td>
<td>20</td>
</tr>
<tr>
<td>No. of nesting attempts</td>
<td>28</td>
<td>43</td>
<td>39</td>
</tr>
<tr>
<td>No. of eggs laid</td>
<td>49</td>
<td>71</td>
<td>59</td>
</tr>
<tr>
<td>No. of eggs hatching</td>
<td>28</td>
<td>44</td>
<td>28</td>
</tr>
<tr>
<td>% nest success</td>
<td>61</td>
<td>53</td>
<td>51</td>
</tr>
<tr>
<td>% chick survival</td>
<td>68</td>
<td>75</td>
<td>86</td>
</tr>
</tbody>
</table>

The sum of the observations of a given activity occurring within 75 m of the nest was calculated and then multiplied by four. Similarly, activity which occurred 75–150 m from the nest was multiplied by three. Chi-square and Mann-Whitney \( U \)-tests were used to test for significant differences (Snedecor and Cochrane 1967).

**RESULTS**

The numbers of pairs fledging two chicks, one chick or no chicks did not differ among years (Table 2; \( \chi^2 = 1.35, \) df = 8, \( P > 0.05 \)). Likewise the number of eggs in successful nests was not different from the number of eggs in unsuccessful nests (Table 2; \( \chi^2 = 0.71, \) df = 2, \( P > 0.05 \)). Two-egg clutches, however, were significantly more successful than one-egg clutches (\( \chi^2 = 6.63, \) df = 1, \( P < 0.05 \)).

Twenty-two nests out of a 3-year total of 110 represented renesting attempts. Initial nest attempts had a success rate of 52% compared to 59% for subsequent attempts (\( \chi^2 = 0.21, \) df = 1, \( P > 0.05 \)). The mean clutch-size of first nesting attempts was 1.76 ± 0.43 compared to 1.55 ± 0.51 in subsequent tries (Mann-Whitney \( U \)-test, \( P < 0.05 \)). Incubation initiated after the third week of June was not as successful as that started earlier (Fig. 2).

There were 4.3 ± 3.1 and 4.6 ± 2.5 nesting sites available per occupied and unoccupied loon territories, respectively (Mann-Whitney \( U \)-test, \( P > 0.05 \)). However, there were significantly fewer potential nesting sites available on occupied territories without nests, 3.17 ± 0.60 than on those with nests, 4.91 ± 2.62 (Mann-Whitney \( U \)-test, \( P < 0.01 \)). When actual use of potential nest-sites is compared to cottage density, use is not different from availability until density reaches five cottages within 150 m of
Table 2

Summary of Egg Production and Fledging Success Per Year

<table>
<thead>
<tr>
<th>Year</th>
<th>Successful nests(^a) with Two eggs</th>
<th>One egg</th>
<th>Unsuccessful nests with Two eggs</th>
<th>One egg</th>
<th>Nesting pairs fledging</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Two chicks</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>One chick</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Zero chicks</td>
</tr>
<tr>
<td>1977</td>
<td>13</td>
<td>2</td>
<td>8</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>1978</td>
<td>23</td>
<td>3</td>
<td>5</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td>1979</td>
<td>10</td>
<td>8</td>
<td>10</td>
<td>11</td>
<td>4</td>
</tr>
</tbody>
</table>

\(^a\) A successful nest is one in which at least one egg hatches.

a site (Table 3). At five or above, loons avoided nest-sites with cottages within 150 m \(\chi^2 = 18.18, \text{ df } = 5, \ P < 0.01\). Hatching success declined as cottage density increased \(\chi^2 = 7.96, \text{ df } = 2, \ P < 0.05\, \text{Table 4, Fig. 3}\) and nest success rates increased with distance from the nearest cottage \(\chi^2 = 8.76, \text{ df } = 3, \ P < 0.05\).

In areas that ranged from totally undeveloped to moderately developed (up to two cottages within 150 m of the nest), 0.78 chicks per egg hatched survived to the fledging stage (95% confidence limit 0.63–0.84). In areas with more than two cottages within 150 m of the nest, 0.75 chicks per egg hatched survived to the fledging stage (95% confidence limit 0.54–0.95);

![Fig. 2. Date of initiation of incubation (data from 1977, 1978, and 1979).](image-url)
Cochrane 1977). The difference between the two areas was not significant, \( P > 0.05 \) (Cochrane 1977:57).

The weighted human activities that occur within 150 m of a nest demonstrate significantly more total activity around developed nests than undeveloped ones (Table 6). There was also a greater number of motorboats, non-motorized water craft, and people on shore (Mann-Whitney U-test, \( P < 0.05 \)).

**DISCUSSION**

The average reproductive success of the Common Loon was consistent over the 3-year period of this study. Despite a slightly smaller percentage of eggs hatched in 1979, a higher percentage of chicks fledged than in the previous 2 years. Compensating for high nest loss is expected in these birds. A study of the Red-throated \((G.\ stellata)\) and Arctic loons indicated that, when food is limited, a pair can more readily rear one chick

### Table 3

**Occupied Loon Territories with Nests**

<table>
<thead>
<tr>
<th>No. of cottages within 150 m of a potential nest-site</th>
<th>No. of potential nest-sites</th>
<th>No. of actual nest-sites</th>
<th>No. actual nests/potential nest-sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>160</td>
<td>40</td>
<td>0.25</td>
</tr>
<tr>
<td>1</td>
<td>59</td>
<td>14</td>
<td>0.24</td>
</tr>
<tr>
<td>2</td>
<td>11</td>
<td>6</td>
<td>0.55</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>6</td>
<td>1.5</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>6</td>
<td>0.43</td>
</tr>
<tr>
<td>5 or more</td>
<td>32</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Total</td>
<td>280</td>
<td>73</td>
<td>—</td>
</tr>
</tbody>
</table>

### Table 4

**Cottage Density and Common Loon Nesting Success**

<table>
<thead>
<tr>
<th>No. of cottages within 150 m of the nest</th>
<th>No. of successful nests</th>
<th>No. of unsuccessful nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>32</td>
<td>17</td>
</tr>
<tr>
<td>1</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>2 or more</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Total</td>
<td>49</td>
<td>35</td>
</tr>
</tbody>
</table>
than two to the fledgling stage (Davis 1972). Yonge (1981) suggested that the second egg of Common Loons is expendable and that two-egg clutches are an adjustment to relatively high loss of eggs or chicks. He also showed that the second chick is more vulnerable to loss than the first.

We also found that two-egg clutches were more successful than one-egg clutches as did Titus and Van Druff (1981). One-egg clutches are more readily abandoned by loons and thus have a lower chance of success (Olson and Marshall 1952).

One of the difficulties in studying nest success related to clutch-size is the problem of not finding all eggs laid. Thus, although we were surveying lakes as soon as the birds arrived back from the south, and began monitoring their nesting habits early, some nests may have lost one egg before we observed it. Yonge (1981) found that virtually all loons laid two eggs but sometimes one was lost. In this study, one-egg clutches may have started with two eggs, however, the majority of the incubation time was spent on one egg.

**Fig. 3.** Percent of breeding pairs of loons with at least one egg hatching vs development within 150 m of a loon nest.
TABLE 5
DISTANCE FROM COTTAGE(S) TO COMMON LOON NESTS

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>No. of successful nests</th>
<th>No. of unsuccessful nests</th>
<th>Percent successful</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–200</td>
<td>27</td>
<td>29</td>
<td>48</td>
</tr>
<tr>
<td>201–400</td>
<td>8</td>
<td>14</td>
<td>36</td>
</tr>
<tr>
<td>401–600</td>
<td>8</td>
<td>5</td>
<td>62</td>
</tr>
<tr>
<td>&gt;600</td>
<td>9</td>
<td>1</td>
<td>90</td>
</tr>
<tr>
<td>Total</td>
<td>52</td>
<td>49</td>
<td>56</td>
</tr>
</tbody>
</table>

Like Yonge (1981) we observed that nests initiated early had a better chance of success. To determine the onset of incubation we aged young birds using plumage characteristics and then added 29 days for the incubation period as reported by Olson and Marshall (1952). More recently Yonge (1981) reported that actual incubation time was 26 days and the 29 days included the interval between egg-laying and onset of incubation. If true, the potential error from aging chicks and backdating to initiation of incubation was up to 6 days rather than the 3 days we thought when we were doing the study. This problem, however, was consistent throughout the study and does not detract from the major conclusion.

The percentage of chicks at the fledgling stage during the first 2 years was similar to the figure of 78% reported by Olson and Marshall (1952) in Minnesota, and 68% by Yonge (1981) from Saskatchewan, but less than the 94.4% observed by McIntyre (1975). The 1979 results were close to

TABLE 6
COMPARISON OF WEIGHTED ACTIVITY WITHIN 150 M OF EIGHT DEVELOPED AND EIGHT UNDEVELOPED COMMON LOON NESTS IN 1979

<table>
<thead>
<tr>
<th>Activities</th>
<th>Average activity in four, 1.5-h visits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Developed nests</td>
</tr>
<tr>
<td>Total activity</td>
<td>81.6</td>
</tr>
<tr>
<td>Large motorboats</td>
<td>14.9</td>
</tr>
<tr>
<td>Non-motorized water craft</td>
<td>16.0</td>
</tr>
<tr>
<td>People on shore</td>
<td>28.4</td>
</tr>
<tr>
<td>Swimmers</td>
<td>0.8</td>
</tr>
<tr>
<td>Fishermen</td>
<td>8.6</td>
</tr>
<tr>
<td>Small motorboats</td>
<td>12.9</td>
</tr>
</tbody>
</table>
the 88.4% reported by Sutcliffe (1978) in New Hampshire. The number of chicks per pair of loons with at least one hatched egg in this study compares favorably with other studies (Olson and Marshall 1952, McIntyre 1975, Sutcliffe 1978, Yonge 1981).

It seems clear that loons can cope with recreational activity of humans, as long as this activity is at a relatively low level. In central Ontario Common Loon reproductive effort is similar to that in other areas and there does not appear to be any significant reduction in the loon's biological ability to produce young. Many cottages and excessive human activity around the nest appear to reduce the probability of young hatching successfully. Once a chick is hatched, however, the parent birds usually move to a relatively quiet spot on the lake. At that point, the probability of success of raising the chick to fledging seems independent of recreational activities at the level studied here.

This conclusion must be modified, however, by the fact that some loons become habituated to human presence. For example, despite the high level of cottage development around a Dickie Lake nest (four cottages within 150 m), the loons reared two chicks to the fledgling stage in both 1978 and 1979. The incubating loons did not flush from the nest even when approached quite closely by canoe, and the offspring of these loons exhibited the same lack of fear of humans. These loons may nest successfully on highly developed lakes, whereas loons with little or no prior exposure to human activity would fail to nest or even to occupy the territory.

During the course of this work we did not actually observe the events which caused nest loss or chick mortality. Most observations of nest loss involve reconstructing the probable cause from evidence at the site (Yonge 1981). Nevertheless, the reduction in nest success near cottages and the higher level of human activity around nests in developed areas certainly suggest that the most probable cause of failure is associated with human activity.

Despite the fact that recreational activity has a negative influence on loon reproductive success, these animals have a considerable ability to adjust to human activity. More investigation into this behavior and how it affects a loon population is needed.

**SUMMARY**

Reproductive success of the Common Loon (*Gavia immer*) in relation to cottage development was studied from 1977–1979 in central Ontario. Two-egg clutches were significantly more successful than one-egg clutches and loons that initiated incubation early in their breeding season tended to be more successful than those that nested later when the risk of human disturbance was greater.

Hatching success declined as the number of cottages within 150 m of the nest increased. Once the eggs had hatched, chick survival appeared to be independent of cottage development around the nest. When human activity near eight nests within 150 m of at least three
cottages were compared to eight nests where there was no development, the difference in human activity was highly significant ($P < 0.01$). It is believed that some loons nesting in developed areas may have become habituated to humans.

ACKNOWLEDGMENTS

Thanks are extended to Brian Ratcliff and Mark Sobchuk for their enthusiastic assistance with the summer field work and to the Ontario Ministry of Municipal Affairs and Housing who financed this work. M. Peterson, K. Bildstein, and J. Cage provided helpful reviews.

LITERATURE CITED


VOCALIZATIONS OF THE WHITE-BREASTED NUTHATCH

GARY RITCHISON

The White-breasted Nuthatch (Sitta carolinensis) is the most widespread nuthatch in North America and has been the subject of several studies (Tyler 1916; Kilham 1968, 1972, 1981; Long 1982). Each study has included descriptions of, and proposed functions for, some of this nuthatch’s vocalizations. However, none of these works featured a description of the complete vocal repertoire.

Herein I describe and analyze all known vocalizations of the White-breasted Nuthatch. A description of the behavioral context of these vocalizations is presented, and possible functions are suggested.

METHODS AND MATERIALS

I studied a population of White-breasted Nuthatches near Elysian, Le Sueur Co., Minnesota, an area of rolling terrain where the dominant trees included hackberry (Celtis occidentalis) and sugar maple (Acer saccharum). Data on vocalizations and associated behavior were collected from 1 October 1973–1 May 1975.

Vocalizations were recorded with either a Nagra IV or Uher 4000 Report-L tape recorder at a tape speed of 19 cm/sec, using an Electro-voice 634A microphone mounted on a 48-cm parabolic reflector. Nest cavity recordings were made using an Electro-voice 644 Sound-Spot microphone mounted near a nest hole. Audiospectrograms were made with a Kay Electric 6061B Sona-Graph. Frequency measurements were made from spectrograms produced with the narrow-band filter and time measurements were made from spectrograms produced with the wide-band filter. The acoustical terminology is that of Mulligan (1963:276).

RESULTS

Adult Vocalizations

Hit and tuck calls.—These calls consisted of single notes with the mean duration of hits being 0.028 ± 0.006 sec (N = 53) and of tucks 0.055 ± 0.010 sec (N = 30). Hits and tucks were easily categorized because (1) no calls of intermediate duration were noted, and (2) hits down-slurred while tucks exhibited a slight upslur (Fig. 1a). Both calls were given at a frequency of ca. 2 kHz.

These calls, the most commonly heard vocalizations of the White-breasted Nuthatch, were given year round but most frequently in autumn and winter. Hits and tucks were given by both sexes and were exchanged by paired nuthatches numerous times daily in winter months. Paired nuthatches are frequently out of sight of each other as they forage and these notes may serve to keep individuals informed as to the location of their
Fig. 1. Spectrograms of various White-breasted Nuthatch vocalizations: (a) hit-tuck; (b) tchup; (c) quank; (d) "discontinuous" quank; (e) quank quank; (f) "rapid" quank; (g) "rough" quank; (h) chrr.
mate. Kilham (1972) suggested that *hits* and *tucks* also serve to maintain pair bonds.

*Tchup call.*—The *tchup* call (Fig. 1b) consisted of a single note averaging 0.056 ± 0.009 sec (N = 31) in duration. This call down-slurred from an average high frequency of 2.12 ± 0.19 kHz (N = 25) to an average low of 1.60 ± 0.15 kHz (N = 25). The call was uttered by individuals of both sexes.

The *tchup* call apparently was used to announce the arrival of an adult outside of the nest hole. After the *tchup* call was given by an adult arriving at the nest hole, young nuthatches always responded with begging calls. Also, during incubation, adult females often responded with *chrr* calls when males gave *tchup* calls outside the nest hole. Kilham (1972, 1981) suggested that *tchup* calls may also be used to express mild excitement.

*Quank calls.*—These vocalizations of the White-breasted Nuthatch have been phonetically rendered as *kun, ka-un, kaan,* or *quank.* Previous authors noted that these calls “are employed when the bird is excited” (Tyler 1916:24) or that they “expressed excitement, the degree depending on whether the notes are single or given in a rapid series and whether loud or soft” (Kilham 1972:117). Five variations of the *quank* call were found in the present study and these are described below.

1) *Quank call.* This call consisted of a single note averaging 0.135 ± 0.035 sec (N = 38) in duration. The entire note had a frequency of about 2 kHz (Fig. 1c). Both sexes gave the call throughout the study period.

Single *quanks* appear to express mild excitement (pers. obs.; Kilham 1972, 1981). These calls were nearly always given when nuthatches were approached by observers while foraging in trees or on a bird feeder.

2) “Discontinuous” *quank call.* The “discontinuous” *quank* call consisted of a series of notes repeated at varying intervals. The individual notes averaged 0.103 ± 0.020 sec (N = 18) in duration and had an average frequency of about 2 kHz (Fig. 1d). Both sexes gave the call throughout the study period.

This call appeared to indicate a somewhat higher level of excitement than the single *quank* call. For example, the discontinuous *quanks* were given when nuthatches sighted a Great Horned Owl (*Bubo virginianus*) or a Barred Owl (*Strix varia*). During the nesting season nuthatches also gave this call when an intruder, generally a gray squirrel (*Sciurus carolinensis*) or human, approached the nest hole.

3) *Quank, quank call.* This vocalization consisted of two *quank* calls given in rapid succession. The first *quank* averaged 0.091 ± 0.003 sec (N = 24) in duration and the second 0.087 ± 0.005 sec (N = 24). The average, between-note duration was 0.068 ± 0.005 sec (N = 24). The call
had a frequency of ca. 2 kHz (Fig. 1c). Both sexes uttered this call through-
out the study period.

The *quank*, *quank* call was given in a variety of circumstances, all of
which indicated a rather high level of excitement. For example, when
nuthatches were scolding Great Horned or Barred owls this call was given
in conjunction with discontinuous *quanks*. In these cases the *quank*, *quank*
call was often given shortly after the nuthatches apparently noticed the
owls. Then, after a few minutes, the *quank*, *quank* calls diminished into
discontinuous *quanks* suggesting a reduction in the level of excitement
(i.e., habituation).

Long (1982:218) noted that male White-breasted Nuthatches sometimes
uttered a call with “paired syllables” (*quank*, *quank*) while performing
displays near the nest induced by the presence of live or mounted pred-
ators. In the present study, a male nuthatch gave the *quank*, *quank* call
after being chased by a Sharp-shinned Hawk (*Accipiter striatus*).

(4) ‘Rapid’ *quank* call.—This vocalization consisted of a rapid series
of 4–18 *quank* calls, with 4–8 being the most common. A greater number
of notes was given in contexts which might be expected to be characterized
by a higher level of excitement. The mean duration of the individual *quank*
notes was 0.066 ± 0.014 sec (N = 44) and the mean internote interval was
0.051 ± 0.004 sec (N = 37). The call was given at an average frequency
of 2 kHz (Fig. 1f). The notes were generally given at a rate of 9.1 ± 1.0
per sec.

Individuals of both sexes gave this call throughout the study period in
a variety of circumstances and it appeared to indicate a rather high level
of excitement. For example, during the breeding season this call was given
when gray or red (*Tamiasciurus hudsonicus*) squirrels approached a nut-
hatch nest hole. Long (1982:218) reported that male nuthatches sometimes
uttered rapid *quanks* (“wawaawaawa”) when performing nest-site dis-
plays to live or stuffed predators.

The rapid *quank* call was often directed toward other nuthatches. On
three occasions males with adjacent territories were observed near their
boundaries addressing rapid *quanks* toward their rivals. This call was also
given by males when nuthatch songs were played back within their territ-
ories. Kilham (1981) referred to the “rapid” *quank* call as the agonistic
song and indicated that it was given when he approached a nest and, on
another occasion, when a male nuthatch approached a Barred Owl.

(5) “Rough” *quank* call.—Another variant of the *quank* call was the rough *quank*. The word “rough” is used to describe the effect that rapid
modulation in frequency has upon the quality of the sound produced. This
call consisted of a series of notes repeated at varying intervals. The in-
Fig. 2. Spectrograms of various White-breasted Nuthatch vocalizations: (a) and (b) phee-oo; (c) "squeal"; (d) brr-a; (e) "whine"; (f) slow song; (g) fast song.
individual notes averaged 0.109 ± 0.005 sec (N = 16) in duration and had an average frequency of ca. 2.3 kHz (Fig. 1g). This call was very similar to the discontinuous quank except for the frequency modulation.

The rough quank call appeared to express the highest level of excitement of any of the quank calls. It was given by individuals of both sexes and was only recorded prior to the nesting period. This call was given along with rapid quanks on the three occasions when males with adjacent territories were observed near the boundaries. Kilham (1981:273) also reported that nuthatches give this call when they come together. He noted that “the vocalizations of 3 or 4 nuthatches in conflict . . . include . . . quavering qua-rr . . . .” The harsh nature of the call (Morton 1977) and the situations in which it occurred suggest that it functions as an agonistic call.

Chrr call.—This call was given only by adult females during the period prior to nesting. It covered a wide range of frequencies (0.5–6.0 kHz; Fig. 1h) and averaged 0.591 ± 0.212 sec (N = 11) in duration.

The chrr call of the adult female was similar in structure to the begging calls of older nestlings (Fig. 3d,e) and appeared to serve the same function, i.e., to elicit feeding. Kilham (1972:121) suggested that in this manner the female “teaches her mate, or more exactly awakens his latent parental instincts, by playing the role of a nestling. . . .”

Phee-oo call.—The phee-oo call (Fig. 2a,b) consisted of a single note with an average duration of 0.235 ± 0.050 sec (N = 31). The call exhibited a gradual downsllr from an average high frequency of 3.45 ± 0.08 kHz (N = 16) to an average low frequency of 1.89 ± 0.24 kHz (N = 16). These calls were not loud, being audible to a distance of 20 m, and were heard only during the mating and nesting period.

The phee-oo call appeared to serve two functions, one of which was the expression of sexual excitement (Kilham 1972). During the present study male nuthatches gave the phee-oo call prior to and during sexual pursuit flights and females gave the call immediately before and after coition. The phee-oo call also appeared to express anxiety. For example, on one occasion a male nuthatch uttered several phee-oos when closely approaching a nuthatch model for the first time (as songs were being played back). Also, females often gave this call when I approached a nest-hole to put up or take down a microphone.

Squear call.—This call (Fig. 2c) was given by four of nine female White-breasted Nuthatches as they were being held or removed from a trap or mist net. None of the 18 males captured during the study uttered this call. The mean duration of the call was 0.247 ± 0.043 sec (N = 14). Other investigators have also noted that females may utter such calls more frequently than males (Rohwer et al. 1976, Balph 1977).
**Brr-a call.**—This call (Fig. 2d) was a trill composed of 2–21 notes of equal pitch (1.8–2.2 kHz). There seemingly was a positive relationship between the number of notes and the level of agonistic behavior. The mean duration of the call was 0.339 ± 0.065 sec (N = 17) with the individual notes averaging 0.014 ± 0.001 sec (N = 27) and the internote interval averaging 0.029 ± 0.006 sec (N = 25).

The brr-a call was directed at both nuthatches and other species. Interspecifically, it was given when another bird, usually a Black-capped Chickadee (*Parus atricapillus*), approached a nuthatch on a feeder and, conspecifically, when a nuthatch model was placed within 1 m of a speaker during playback of nuthatch songs. On the four occasions when playback was used, males approached to within a few cm of a study skin, assumed the aggressive threat posture described by Kilham (1981), and gave the brr-a call. Many other species of birds have been found to utter low, harsh sounds in an aggressive context (Morton 1977).

**“Whine” call.**—This call (Fig. 2e) consisted of a single note averaging 0.204 ± 0.022 sec (N = 7) in duration. It exhibited a gradual downswept from an average high frequency of 2.09–0.15 kHz (N = 7) to an average low frequency of 1.84 ± 0.19 kHz (N = 7). Males uttered the call more frequently than females (six of seven observations).

The “whine” call frequently preceded the brr-a call and was given in situations similar to those in which the brr-a call was given, e.g., when another bird approached a nuthatch on a bird feeder or when playback of song was used with a model. Unlike the brr-a call, the aggressive threat posture did not accompany the “whine” call.

**Song.**—The song of male White-breasted Nuthatches has been described as “a regular series of about six to eight notes, sometimes more sharply accented, striking the same pitch, each with a slight rising inflection” (Bent 1948:8) and has been variously rendered into syllables such as *hah-hah-hah* and *what-what-what* (Allen 1912). Kilham (1972) described the song as a rapid series of 8–11 *what* notes or musical *wurps*. These descriptions generally correspond to what I have termed the slow song. Other authors (Tyler 1916, Bent 1948) have also described a variation of the song (which I have designated the fast song) in which 20–30 notes are crowded into the same amount of time as the 8–11 occupy in the slow song.

The slow variant consisted of a series of notes, generally 9–11, given at an average rate of 6.7 ± 1.0 notes per sec (N = 38). The individual notes, each with a slight rising inflection, averaged 0.095 ± 0.010 sec (N = 77) in duration and the internote interval averaged 0.065 ± 0.007 sec (N = 70) in duration. Slow songs were given at frequencies between 1.5 and 2.0 kHz (Fig. 2f).
The fast variant consisted of a longer series of notes, generally 16–26, given at an average rate of $11.5 \pm 0.5$ notes per sec ($N = 38$). The individual notes, each with a slight rising, then falling, inflection, averaged $0.053 \pm 0.004$ sec ($N = 42$) in duration and the internote interval averaged $0.036 \pm 0.003$ sec ($N = 38$) in duration. The dominant frequencies of the fast songs were between 1.9 and 2.5 kHz (Fig. 2g).

The two song variants of the White-breasted Nuthatch appeared to function in the same context. General observation suggested that, as with other nuthatch vocalizations, the speed of delivery was related to the level of excitement, i.e., an increased speed of delivery indicated a higher level of excitement.

The song of the White-breasted Nuthatch apparently serves the same functions as the songs of many other species, i.e., territorial defense and courtship. However, Kilham (1972:126) noted that while the song of the nuthatch may serve to advertise territory it “differs in a number of ways from those of more classically described species in being sung in most sustained fashion in mid-winter . . . and . . . in the male nuthatch addressing his song to his mate rather than to rival males.”

Vocalizations of the Young

“Begging” calls.—The “begging” call of young White-breasted Nuthatches exhibited gradual change throughout development. This call (Fig. 3a) first appeared within 24 h after hatching and was quite variable in both duration (0.09–0.16 sec) and frequency (4–6 kHz). Between 3–7 days post-hatching the call (Fig. 3b) lengthened ($\bar{x} = 0.183 \pm 0.009$ sec, $N = 9$) and covered a wider range of frequencies.

On about the eighth day post-hatching, the begging call developed a raspy component, i.e., part of the call covered a wide range of frequencies (Fig. 3c) and had a harsh sound. The terminal part of this call resembled the earlier begging call in its frequency (4.5–5.5 kHz) and absence of harmonics. This call was longer in duration (0.19–0.30 sec) than the above mentioned calls.

As the nestlings grew older the raspy component of the begging call became more apparent and harmonics appeared in the latter portion of the call (Fig. 3d). The call also continued to lengthen (0.35–0.43 sec). By the 14th day post-hatching the begging call was composed entirely of the raspy component and covered an extremely wide range of frequencies (0.5–6.0 kHz) with the fourth harmonic being dominant (Fig. 3e). At this time the juvenile begging call closely resembled the chrr call of the adult female (Fig. 1h) and was variable in duration.

“Juvenile squeal” call.—This call (Fig. 3f) consisted of a single note averaging $0.146 \pm 0.023$ sec ($N = 11$) in duration. The call showed a grad-
Fig. 3. Spectrograms of various White-breasted Nuthatch vocalizations: (a) “begging” call (24 h); (b) “begging” call (3–7 days); (c) “begging” call (8 days); (d) “begging” call (11 days); (e) “begging” call (14 days); (f) “squeal.”
ual drop in frequency from an average high of $2.47 \pm 0.16$ kHz ($N = 11$) to an average low of $2.05 \pm 0.05$ kHz ($N = 11$).

This call was given by a 24-day-old female while being held. Although young nuthatches were handled on several occasions, this was the only time that the call was given. Whether this was due to the absence of the appropriate stimulus or to the fact that the call had not previously been a part of the nestling's repertoire is unknown; however, whereas adult nuthatches usually flew from the immediate area when nestlings were removed from the nest, on this occasion they remained nearby and gave rapid quank calls.

**DISCUSSION**

The vocal repertoire of the White-breasted Nuthatch was found to consist of 15 distinct types of calls and a song that was given at two different rates. Of these calls, adults gave 13 and the young two. When the similarities between the calls are considered, it appears the nuthatches may have only nine basic calls, with the remaining four calls comprising variations of some of these basic calls. The “discontinuous” quank, quank, quank, “rapid” quank, and “rough” quank appear to be variations of the basic quank call, with each variant being indicative of a different level of excitement. The two song variants may similarly reflect different excitement levels.

Most of the functional categories of calls found in other passerines were detected in the repertoire of the White-breasted Nuthatch (cf. Thorpe 1961:37). I did not note an alarm call specific to flying predators; however, nuthatches did appear to respond to the aerial warning call of the Black-capped Chickadee. On one occasion several chickadees gave the warning note described by Odum (1942) and Ficken et al. (1977) when a Sharp-shinned Hawk flew over the area. The nuthatches, as well as the chickadees, remained motionless. Other investigators have reported that birds of one species may respond to the warning calls of another species (e.g., Thorpe 1961, Van Tyne and Berger 1976).

Various studies (e.g., Thorpe 1961, Armstrong 1963) have shown that vocalizations with similar functions have similar structures. For example, the scolding calls of most birds cover a wide range of frequencies, a characteristic that makes the calls easy to locate, whereas warning calls generally have a relatively narrow and high frequency range, a trait that makes the call difficult to locate. The structure of nuthatch vocalizations similarly is related to their function. In situations where it appears to be advantageous for the nuthatch to be easily located, calls cover a wide range of frequencies, e.g., the begging calls of newly-fledged young and the brr-a call. In situations where nuthatches may be vulnerable (nestlings), vocalizations cover a narrow range of frequencies.
Descriptions of the vocalizations of Red-breasted (S. canadensis) and European (S. europaea) nuthatches indicate close similarity between their vocal repertoires and the repertoire of the White-breasted Nuthatch. Kilham (1973:607) compared the vocalizations of White-breasted and Red-breasted nuthatches and found their repertoires to be surprisingly similar. In fact, he stated that “one might expect a greater divergence considering that they are both congeneric and sympatric.” Lohrl’s (1958) description suggests that the vocalizations of the European Nuthatch also bear a great similarity to those of the White-breasted Nuthatch. Verbal descriptions, however, have obvious limitations and spectrographic analysis will be necessary to make more definitive comparisons.

SUMMARY

Vocalizations of the White-breasted Nuthatches (Sitta carolinensis) were studied from 1 October 1973–1 May 1975 in Le Sueur County, Minnesota. The vocal repertoire of this nuthatch was found to consist of two juvenile and 13 adult calls plus a song that was given at two different rates. A description of the behavioral context of the vocalizations is presented, and possible functions are suggested.

ACKNOWLEDGMENTS

I would like to thank M. Frydendall for advice and encouragement both during this study and throughout my years at Mankato State. I would also like to thank S. and D. Ritchison for assistance in the field and D. J. Martin, and an anonymous reviewer for many helpful comments on the manuscript. I appreciate the assistance of J. Ward and T. Rhodus in the preparation of the figures and of B. Rupard in the typing of the manuscript. This study was supported in part by a Mankato State University Research Fund Grant.

LITERATURE CITED


DEPT. BIOLOGY, MANKATO STATE UNIV., MANKATO, MINNESOTA 56001. (PRESENT ADDRESS: DEPT. BIOLOGICAL SCIENCES, EASTERN KENTUCKY UNIV., RICHMOND, KENTUCKY 40475). ACCEPTED 1 MAR. 1983.
GENERAL NOTES

A dietary overlap of Evening Grosbeaks and Carolina Parakeets.—The known winter range of Evening Grosbeaks (Coccothraustes vespertuinus) in eastern North America has increased dramatically in the past 90 years. As a result of the range spread, the birds have encountered a variety of habitats for the first time. Among these habitats are extensive bottomland forests and cypress swamps in the southern states. On 3 December 1977 Brunswig and Winton saw 12 grosbeaks in the top of a large bald cypress (Taxodium distichum) in the interior of the Francis Beidler Forest, a sanctuary of the National Audubon Society and the Nature Conservancy in Berkeley and Dorchester counties, South Carolina. The observers' attention was drawn to the birds when fragments of cypress cones began to rain into the water. Closer inspection revealed that the birds were feeding on cypress fruits or seeds. Later that same winter, Robertson (Florida Field Nat. 7:11, 1979) noted similar feeding behavior by Evening Grosbeaks in Florida.

We can find no other record of the use of this food source by these birds. Our search of the literature revealed few other vertebrate species that eat cypress fruit or seeds: gray squirrels (Sciurus carolinensis) (Gunderson, Regeneration of cypress, Taxodium distichum and T. ascendens, in logged and burned cypress stands at Corkscrew Swamp Sanctuary, Florida. M.S. thesis, Univ. Florida, Gainesville, Florida, 1977), three species of ducks (Anatidae) and Sandhill Cranes (Grus canadensis) (Landers et al., J. Wildl. Manage. 41:118-127, 1977; Martin et al., American Wildlife and Plants, McGraw-Hill Book Co., New York, New York, 1951), and Wild Turkeys (Meleagris gallopavo) (Powell, The Florida Wild Turkey, Florida Game and Freshwater Fish Comm. Tech. Bull. 8, 1965). None of these authors listed another important cypress seed predator in historical times, namely the Carolina Parakeet (Conuropsis carolinensis), although cypress mast was an important winter food (Bent, U.S. Natl. Mus. Bull. 176, 1940). We speculate that only Evening Grosbeaks and Carolina Parakeets among North American birds have or had the ability to crack open cypress cones and other very hard food items. Other similarities in diet between the two species are numerous. Both extensively cat (ate) buds, pine mast, maple seeds, a variety of fruits, seeds of fruits, and other seeds (Speirs, pp. 206-237 in Bent and Austin, eds., U.S. Natl. Mus. Bull. 237, Pt. 1, 1968; McKinley, unpubl. and pers. comm.).

Carolina Parakeets were widely distributed in pre-Colonial eastern North America, north in winter to the Ohio River valley and, occasionally at least, to Albany, New York (McKinley, Jack-Pine Warbler 55:106-124, 1977). Consequently, after the extinction of Carolina Parakeets (McKinley, Indiana Audubon Quart. 58:8-18, 50-61, 103-114, 1980) certain winter foods in eastern North America available only to them (and to the similarly strong-billed Evening Grosbeaks) were not routinely harvested by avian predation. It is possible, and seems to us plausible, that the demise of the Carolina Parakeets may have been a contributory antecedent to the winter range expansion of the Evening Grosbeaks in North America.

Acknowledgments.—This manuscript has benefited from the criticism of D. McKinley, D. H. Speirs, R. F. Harlow, A. E. Ross, D. McNair, J. L. Beacham, and M. C. Hamel. — NORMAN L. BRUNSWIG, STEPHEN G. WINTON, NATIONAL AUDUBON SOCIETY, FRANCIS BEIDLER FOREST, RT. 1, BOX 114, HURLEYVILLE, SOUTH CAROLINA 29448; AND PAUL B. HAMEL, DEPT. ZOOLOGY, CLEMSON UNIV., CLEMSON, SOUTH CAROLINA 29631. ACCEPTED 2 NOV. 1982.
On the relationship between breeding bird survey counts and estimates of male density in the Red-winged Blackbird.—The annual North American Breeding Bird Survey (BBS) developed in the United States in 1964 began in Canada in 1966 (Erskine. The first 10 years of the co-operative breeding bird survey in Canada, Can. Wildl. Serv., Rept. Ser. No. 42, 1978). The BBS is potentially valuable as an aid to research in population dynamics since surveys are conducted across the continent, are censused according to a standard methodology, and the same routes may be sampled annually over many years. Shortcomings of the survey, including sources of error, have been addressed by Weber and Theberge (Wilson Bull. 89:543–560, 1977) and Erskine (1978).

The BBS provides a source of data from which trends in species numbers have been derived, but Erskine (1978) has warned against using these counts as indicators of species density. Temporal-spatial changes in blackbird (Icterinae) and Eurasian Starling (Sturnus vulgaris) population indices derived from BBS counts have been assessed by Dolbeer and Stehn (Population trends of blackbirds and starlings in North America, 1966–76. U.S.D.I., Fish Wildl. Serv., Spec. Sci. Rept. Wildl. No. 214, 1976). BBS data have also been integrated into computer models designed to facilitate decision-making regarding the possible killing of millions of blackbirds and starlings (Dolbeer et al., Proc. Vert. Pest Conf. 7:35–45, 1976). Central to these endeavors have been the assumptions that: (1) changes in BBS counts reflected actual changes in population densities (levels), and (2) a substantial positive correlation existed between BBS counts and densities at least as they relate to the above species.

Intuitively, these assumptions seem reasonable, although neither the degree of correlation nor the form of the relationship have been substantiated. Employing data from independent studies conducted in separate years and from widely-separated regions, Dolbeer et al. (1976) derived a curvilinear association between BBS counts and estimates of male Red-winged Blackbird (Agelaius phoeniceus) density. The logarithmic relationship derived showed that, with increasing increments in BBS red-wing counts, there was a reduced rate of increase in estimated male density as density approached 30 males/km². Presumably, regions having large male density values were associated with areas of high habitat suitability (Fretwell and Lucas, Acta Biotheor. 19:16–36, 1969) which, in turn, attracted proportionately more females or sub-adult males; thus, BBS counts of all red-wings increased more rapidly than male density. A better understanding of the relationship between BBS values and estimates of breeding (male) density is necessary if BBS data are to be used effectively in population studies, not only of Red-winged Blackbirds, but ultimately for other species as well. Thus, we collected data over a broad region of southwestern Quebec that would allow comparison of BBS and estimated male density values over the complete range of red-wing densities likely to be encountered. Our aim was to determine the degree of correlation, if any, between BBS red-wing counts and male density estimates, and to identify the form of that relationship.

Methods.—Between 20 June–1 July 1980, estimates of male red-wing density were made along eight BBS routes within the agricultural zone along the St. Lawrence River Valley from Montreal to Quebec City (Weatherhead et al., Phytoprotection 61:39—47, 1980). BBS routes were 40-km transects travelled by motor vehicle and comprised 50 stops made at 0.8-km intervals (Erskine 1978). At each stop an observer recorded all birds seen or heard in 3 min. Counts were totalled after 10 stops, thus five 10-stop summary totals were obtained for each BBS route. Further details may be found in Weber and Theberge (1977) and Erskine (1978). A total of 24, 2.5-km-long, roadside censuses were conducted to estimate male density (Hewitt, J. Wildl. Manage. 31:39—47, 1967; Weatherhead et al. 1980). The roadside census technique involved estimating the total number of territorial male red-wings within 75 m of the roadside using a modified capture-mark-recapture method (Hewitt 1967). Since the area

Table 1
The Mean Percentage (t), Standard Error (SE), and Range of Nine Habitats Encountered on 24 Census Routes Along Eight BBS Routes in Southern Quebec, June 1980

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Percentage of land use</th>
<th>t ± SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hay</td>
<td>22.8 ± 4.2</td>
<td>4.7-36.9</td>
<td></td>
</tr>
<tr>
<td>Cultivation (crops)</td>
<td>13.0 ± 4.5</td>
<td>3.0-36.8</td>
<td></td>
</tr>
<tr>
<td>Pasture</td>
<td>12.1 ± 3.8</td>
<td>0.0-25.6</td>
<td></td>
</tr>
<tr>
<td>Farm</td>
<td>5.9 ± 1.7</td>
<td>0.0-10.9</td>
<td></td>
</tr>
<tr>
<td>Old fields</td>
<td>3.7 ± 1.7</td>
<td>0.0-14.7</td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>16.5 ± 7.4</td>
<td>0.9-50.0</td>
<td></td>
</tr>
<tr>
<td>Water (edge)</td>
<td>4.2 ± 1.8</td>
<td>0.0-13.1</td>
<td></td>
</tr>
<tr>
<td>Urban</td>
<td>14.3 ± 6.0</td>
<td>0.5-50.0</td>
<td></td>
</tr>
<tr>
<td>Miscellaneousa</td>
<td>7.1 ± 3.9</td>
<td>0.3-33.5</td>
<td></td>
</tr>
</tbody>
</table>

*a Includes orchards, fallowfields, ditches, and, on one route, a sparsely wooded peat bog.

censused was a known constant, it was possible to derive an estimate of male density for each roadside census. In addition to these distinctions, a major difference between the BBS and roadside censuses was that the latter method involved continuous counts of males and repeated sampling of the same route, whereas the BBS method relied on single counts at 0.8-km intervals. Along each BBS route starting points for the roadside censuses were chosen at random from the set of BBS stops between stops 1 and 46. Since roadside censuses overlapped four BBS stops, censuses could not be initiated beyond BBS stop 46 nor extend beyond stop 50. Overlap in roadside census strips along each BBS route was not permitted. One BBS route had two roadside censuses, six routes had three censuses, and one route had four censuses. Censuses were done consistently by two observers and, to be in keeping with BBS regulations (Erskine 1978), were conducted in good weather during June. Following each census, habitats adjacent to the route were recorded at 0.16-km intervals.

Table 2
The Mean (t) BBS Count and Male Density, Coefficients of Variation (CV) and Ranges for Red-winged Blackbirds Based on 24 Independent Samples and Pooled Data for Eight BBS Routes, Southern Quebec, 1980

<table>
<thead>
<tr>
<th>Source</th>
<th>N</th>
<th>BBS counts</th>
<th>Male densitya</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>X</td>
<td>CV</td>
</tr>
<tr>
<td>Independent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>census routesb</td>
<td>24</td>
<td>43.5</td>
<td>92.9</td>
</tr>
<tr>
<td>Pooled per</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BBS route</td>
<td>8</td>
<td>206.5</td>
<td>76.3</td>
</tr>
</tbody>
</table>

*a Males/km².
*b Data are 10-stop summary totals for BBS counts.
Two analyses were performed: (1) 10-stop summary totals were correlated with comparable roadside density estimates, and (2) total BBS counts were correlated with averaged male densities censused on that route. The 10-stop summary totals and comparable roadside density estimates referred to the summed data from the 10 BBS stops overlapping most closely with the census routes used to derive the roadside density estimate, while in the second analysis the total red-wing count for each BBS route was correlated with the mean density derived from averaging the density estimates for censuses conducted along that route. Spearman rank correlation coefficient ($R_s$) and both linear and curvilinear least squares regression models were computed for each analysis (Zar, Biostatistical Analysis, Prentice-Hall Inc., Englewood Cliffs, New Jersey, 1974). The linear and curvilinear models were compared with respect to coefficients of determination ($R^2$) in order to assess the relevance of the model proposed by Dolbeer et al. (1976) when applied to data at the regional level (i.e., southwestern Quebec).
Habitat.—Census routes traversed many habitats, but agricultural land use (hay, cultivation, pasture, farm) was predominant (Table 1). Forested and urban areas dominated (50%) the censuses on two BBS routes, while another route crossed a sparsely-wooded peat bog (33% miscellaneous). Although BBS routes were 40 km in length and census routes had a mean length of 7.5 km (about 19% of the BBS route), the values in Table 1 should be reasonably representative given that initiation points were randomly selected. Information regarding land use characteristics was considered important because the BBS count and density estimate relationships described below may be quite different from intensively cultivated to non-agricultural areas.

BBS red-wing counts and estimates of male density.—Overall, estimated density of males averaged 27 individuals per km² in 1980 (Table 2). Wide ranges in BBS counts and density estimates were obtained, but densities had slightly smaller coefficients of variation. It was
possible that the differences in methodologies alone accounted for this consistent decrease in variation.

There was a significant positive correlation ($R = 0.654$, $N = 24$, $P < 0.001$) between summary counts and male density (Fig. 1). A simple linear regression was also significant ($F = 34.8; df = 1, 22; P < 0.001$):

$$\text{density} = 7.33 + (0.443 \pm 0.075 \text{ SE [summary count]}), \quad R^2 = 0.613 \quad \text{(model 1)}.$$

Both the rank correlation ($R = 0.631$) and the linear regression ($R^2 = 0.346$) remained highly significant ($P < 0.005$) even with one apparent outlying data point removed (Fig. 1). These results indicated that male density along a BBS route may be predicted from respective 10-stop summary totals with a significant level of precision. A curvilinear (power) model did not substantially improve the predictive ability ($R^2 = 0.617$, a difference of 0.004); therefore, the linear model was considered adequate. One major reason the degree of correlation was likely not greater was the overlap of census routes with four, rather than all 10, BBS stops. This analysis illustrated that, for the study of red-wing responses to current land use practices and/or land use change, one could employ the 10-stop summary totals to obtain five sampling units per BBS route and thereby improve the level of replication (i.e., sample size). This could be important for analyses in regions where relatively few BBS routes have been conducted annually.

The total number of red-wings per BBS route and estimates of male density were strongly positively correlated ($R = 0.905$, $N = 8$, $P < 0.01$; Fig. 2). A simple linear regression provided considerable precision in predicting male density from the BBS route total ($F = 21.2; df = 1, 6; P < 0.01$):

$$\text{density} = 7.24 + (0.095 \pm 0.02 \text{ SE [BBS count]}), \quad R^2 = 0.780 \quad \text{(model 2)}.$$

An improvement in $R^2$ of 4.8% resulted from a curvilinear power function ($F = 30.0; df = 1, 6; P < 0.01$) suggesting that male density increased more slowly than BBS counts at higher values (Dolbeer et al. 1976); however the slowdown was very minimal (Fig. 2):

$$\text{density} = 0.15 ([\text{BBS count}]^{0.971 \pm 0.18 \text{ SE}}), \quad R^2 = 0.828 \quad \text{(model 3)}.$$

Because this $R^2$ increment was not significant ($F = 1.71, P > 0.05$, Zar 1974:271), due to

<table>
<thead>
<tr>
<th>Year</th>
<th>Estimated density</th>
<th>Predicted density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N$</td>
<td>$\hat{x} \pm SE$</td>
</tr>
<tr>
<td>1980</td>
<td>24</td>
<td>26.6 ± 4.7</td>
</tr>
<tr>
<td>1979</td>
<td>21b</td>
<td>30.0 ± 4.9</td>
</tr>
<tr>
<td>1978</td>
<td>37</td>
<td>39.0 ± 5.6</td>
</tr>
<tr>
<td>1977</td>
<td>32</td>
<td>34.8 ± 2.7</td>
</tr>
</tbody>
</table>

a Males/km$^2$.
b Recalculated using only the seven routes which were run in all 4 years.
the relative ease of formulating the linear model, and because of the minimal slowdown in density increase at higher BBS values, we felt justified in using the simple linear regression in the following test.

Test of model 2.—An ideal test of model 2 was to compare estimates of male density from southwestern Quebec with values predicted from the model using BBS red-wing counts as input data. To this end, we used BBS counts and roadside census data for the years 1977–1979. The roadside census data were those used by Weatherhead et al. (1980) and were thus unrelated to the census data used to generate the model. For this analysis, a subset of roadside census routes was selected each year to minimize the distance between roadside and BBS routes and thereby reduce biases associated with land use changes or other spatially variable factors. This objective was achieved by pooling male densities from roadside census routes within 30 km of BBS routes. BBS red-wing counts were used to predict male density and then these predicted values were used to compute a mean male density for the year. To avoid unknown biases due to missing data, we employed the seven BBS routes which were completed in all 4 years (Table 3).

The 1977 and 1979 predicted densities were close to the independent estimates based on actual censuses of male red-wings and differed by ca. 5.7 males/km², while the largest discrepancy (7.7 males/km²) occurred in 1978 (Table 3). Note that the predicted density varied directly with estimated density during the period 1977–1980, but the magnitudes of the change were unrelated. For example, although the estimated and predicted densities declined between 1977 and 1978 and then increased from 1978–1979, the predicted density in 1979 rose above the predicted 1977 level; whereas, the estimated density in 1979 remained below the estimated 1977 level (Table 3). Finally, we calculated the mean and variation in male density for the years 1977–1979 using all census routes conducted in southwestern Quebec, and compared these with values for the subset described above and shown in Table 3. Overall, regional male red-wing density averaged 28.7 (SD = ±14.8, N = 114) in 1977; 22.6 (SD = ±16.0, N = 104) in 1978; and 36.4 (SD = ±22.3, N = 59) in 1979. The means and variances of the subset were not significantly different (t-tests and F-tests, P > 0.05) from respective overall values.

The estimated and predicted densities were similar given that, other than in 1980, census and BBS routes did not overlap. Thus, effects due to differences in habitat were unavoidable. In addition, the range in estimated male densities during 1977–1979 (24.8–39.0, Table 3) was slightly less than the range calculated from a further subset of 23 census routes sampled all 3 years (20.7–37.1). The latter subset of census routes varied relatively little with respect to habitat between 1978 and 1979, although significant differences in male density were evident (Clark and Weatherhead, unpubl.). Moreover, red-wing populations may undergo an annual redistribution known as the “checkerboard effect” (Rotenberry and Wiens, Oecologia 47:1–9, 1980), especially if red-wings are not habitat limited.

The degree of variation in red-wing estimates observed in this study raises serious questions about sampling precision, not only for the BBS but for the census routes as well. From the coefficients of variation in Table 2, censuses of male density were associated with more stable variances. More importantly, it was evident from the comparison of the subset of roadside censuses used in the test of model 2 with the overall regional set that variation did not change significantly with the addition of two to three times more census routes. Clearly, red-wing populations exhibited substantial tempo-spatial variability. Nevertheless, male red-wing density can be predicted from BBS counts if one applies the model(s) to data from similar landscapes. We echo Weber and Theberge’s (1977) suggestion that general habitat information be collected along BBS routes. At the regional level, a linear relationship between BBS counts and male densities was appropriate; our analyses provided little support for the strongly curvilinear model of Dolbeer et al. (1976). Some caution must be exercised in in-
terpreting population indices from BBS data. For example, if BBS indices indicated yearly increases, our results suggest that one could infer that the population had indeed increased but one could only speculate on the magnitude of the change unless additional supportive information, e.g., important habitat changes, was available. While we believe that male density can be derived from BBS counts via the statistical models presented, and subjected to the logical constraints defined above, we acknowledge that neither predictive models nor single-sample surveys can replace carefully implemented censuses of bird populations (Wiens, Am. Nat. 117:90-98, 1981). This study demonstrated that BBS counts can be extremely useful in deriving estimates of male red-wing density; further research appears warranted to determine the nature of the relationship between BBS counts and (male) densities for other species.

Acknowledgments.—R. Dolbeer, H. Greenwood, and J. Rotenberry suggested several improvements of earlier drafts of this manuscript. S. Wendt and I. Price of the Canadian Wildlife Service, Ottawa, kindly provided BBS results. It is a pleasure to thank M. McIntosh for allowing RGC to help conduct a BBS route, and M. Silverstone for field assistance in 1980. This study would not have been possible without the efforts of BBS volunteers and the technicians who conducted census routes. Financial support was provided by Agriculture Canada and the Ministere de l’Agriculture du Quebec, and by a scholarship to RGC from the Ministere d’Education du Quebec. Computing costs were paid by the Faculty of Graduate Studies and Research, McGill University.—ROBERT G. CLARK, Dept. Renewable Resources, Macdonald Campus of McGill Univ., 21111 Lakeshore Rd., Ste. Anne de Bellevue, Quebec H9X 1C0, Canada; PATRICK J. WEATHERHEAD, Dept. Biology, Carleton Univ., Ottawa, Ontario K1S 5B6, Canada; and RODGER D. TITMAN, Dept. Renewable Resources, Macdonald Campus of McGill Univ., 21111 Lakeshore Rd., Ste. Anne de Bellevue, Quebec H9X 1C0, Canada. (Present address RC: Oikos Ecological Research Associates Ltd., P.O. Box 8818, Saskatoon, Saskatchewan S7K 6S7, Canada.) Accepted 20 Jan. 1983.


Calculating incubation periods of species that sometimes neglect their last eggs: the case of the Sora.—Most investigators follow Heinroth (J. Orn. 70:172–285, 1922) and Nice (Condor 56:173–197, 1954) in determining the shortest normal incubation periods of birds by calculating the time elapsed between laying of the last egg to hatching of the last young in nests in which all eggs hatch (and preferably in which each egg is marked individually on the day of laying). Usually hatching occurs between successive visits to a nest by the observer, so any estimate of the incubation period of a clutch should be accompanied by a “margin of error” (Nolan, Ornithol. Monogr. No. 26, 1978). The Heinroth-Nice method standardizes the incubation periods of free-living birds reported in the literature, applies to most species with different hatching schedules, and minimizes the uncertainty concerning the time when attending adults begin incubating.

We describe here a modified Heinroth-Nice procedure that is recommended for determining the minimal normal incubation periods in large-brooded species which sometimes neglect the last one or two eggs in a nest causing them to hatch later than they otherwise would have (Nice 1954:173; this study). We examine this problem using the Sora (Porzana carolina) as an example.

The Sora has a clutch-size of 5–15 eggs (9–12 is a more typical range) and incubation and care of young is shared by the sexes (Pospichal and Marshall, Flicker 26:2–32, 1954; Tanner and Hendrickson, Iowa Bird Life 26:78–81, 1956). During the hatching period, one adult
Table 1

**Egg Neglect in a Sora Nest and Use of Modified and Unmodified Heinroth-Nice Procedures for Determining Sora Incubation Periods**

<table>
<thead>
<tr>
<th>Nest-cycle variable</th>
<th>Data on nest</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date first egg laid, last egg</td>
<td>22 May, 31 May</td>
<td>Laid one egg/day; clutch-size 10</td>
</tr>
<tr>
<td>Start of hatching, eggs 1–4</td>
<td>12 June, 16:55–13 June, 09:45</td>
<td>Synchronous hatching; assumed start of incubation, laying of egg 4 (see text)</td>
</tr>
<tr>
<td>Hatching sequence, eggs 5–8</td>
<td>one egg/day</td>
<td>Asynchronous hatching between successive visits ca. 1 day apart</td>
</tr>
<tr>
<td>Hatching, egg 9</td>
<td>18 June, 17:05–19 June, 10:30</td>
<td>Egg neglect, skipped ca. 1 day between eggs 8 and 9</td>
</tr>
<tr>
<td>Hatching, egg 10</td>
<td>20 June, 07:45–21 June, 11:00</td>
<td>Egg neglect, skipped ca. 1 day between eggs 9 and 10</td>
</tr>
<tr>
<td>Total hatching interval (h)</td>
<td>187.9 ± 22.03</td>
<td>From hatching of first egg to hatching of last egg ± margin of error*</td>
</tr>
<tr>
<td>Incubation periods*, eggs 4–10 (h)</td>
<td>450.3 ± 8.42</td>
<td>Modified Heinroth-Nice estimate of incubation period, egg 4</td>
</tr>
<tr>
<td>Egg 5</td>
<td>450.3 ± 10.62</td>
<td></td>
</tr>
<tr>
<td>Egg 6</td>
<td>450.3 ± 9.21</td>
<td></td>
</tr>
<tr>
<td>Egg 7</td>
<td>450.3 ± 12.97</td>
<td></td>
</tr>
<tr>
<td>Egg 8</td>
<td>454.4 ± 15.13</td>
<td></td>
</tr>
<tr>
<td>Egg 9</td>
<td>475.8 ± 8.71</td>
<td></td>
</tr>
<tr>
<td>Egg 10</td>
<td>495.4 ± 13.63</td>
<td>Unmodified Heinroth-Nice estimate of incubation period, egg 10</td>
</tr>
</tbody>
</table>

* On several early morning visits to the nest during egg-laying, the egg laid that day had already been deposited; for purposes of calculating incubation periods and their margins of error (Nolan 1978:235), we use 06:00 as an arbitrary and standardized laying time for all eggs.

continues to incubate the remaining eggs in the nest while the other stays with the incomplete brood nearby (Walkinshaw, Auk 57:153–168, 1940).

Soras initiate incubation at least 3 days before the last egg is laid. Within this span start of incubation can be quite variable, having been reported from laying of the first egg (evidently unusual) to laying of the ninth egg in large clutches (Pospichal and Marshall 1954:15; Walkinshaw 1940:158). Thus, not only is spread of hatching between first and last eggs similarly variable between Sora nests, but Soras typically exhibit a mixed hatching schedule in which a first batch of eggs hatch synchronously and the rest hatch asynchronously. Often the eggs in the latter group hatch as they were laid, one each day. However, some birds attending the last few unhatched eggs in nests appear to modify their incubation behavior and cause the ultimate or penultimate and ultimate eggs to miss days before hatching. Application of the last egg rule in such instances will overestimate minimal incubation periods.

**Modified Heinroth-Nice procedure.**—When several eggs in large clutches hatch on the first day of hatching and the rest hatch asynchronously as in the Sora, we assume that full incubation begins with deposition of the last egg in the group to hatch synchronously. We
suggest that the Heinroth-Nice procedure is best applied in the Sora (and in other species that similarly exhibit egg-neglect) by calculating the incubation period for the egg laid on the day that incubation begins. This is equivalent to current practice in groups of birds in which all eggs hatch synchronously (within one 24-h period). By extension, if all eggs hatch asynchronously as they were laid, one can assume that incubation begins with the first egg and that its incubation period is a representative minimal period for the clutch.

Since egg neglect should affect only the last few eggs to be laid in a Sora nest, incubation periods calculated for the first several eggs laid after incubation begins may well be similar (Table 1). But, for purposes of standardization, any method employed should be used consistently.

In two Sora nests that we recently observed on Long Island, New York (Greenlaw and Miller, Kingbird 32:78-84, 1982), we found evidence of egg neglect affecting the hatching time of the last one or two eggs. We have full data on laying and hatching schedules for only one of these nests, so we use it here to illustrate the applications of unmodified and modified Heinroth-Nice procedures for determining minimal incubation periods (Table 1).

In this nest, 10 eggs were laid, one each day. Incubation began with laying of egg 4 (eggs 1-4 hatched synchronously). Eggs 5-8 hatched on a daily schedule, but eggs 9 and 10 each missed a day before hatching. Using egg 4 as the representative egg (modified procedure), the incubation period for this nest is 18.8 ± 0.35 days. This value is close to the mean period of 18.7 days reported by Pospichal and Marshall (1954) for a sample of 22 Sora nests. An indiscriminate use of the unmodified procedure (egg 10) for our nest yields a period of 20.6 ± 0.57 days, a value which lies near the upper end of the range of reported values for this species (Pospichal and Marshall 1954; Tanner and Hendrickson 1956; Walkinshaw 1940; Auk 74:496, 1957).

These observations were made in the course of a continuing investigation of marshland sparrows in the genus *Ammodramus* supported by funds from the Faculty Research Committee of C. W. Post Center, Long Island University. We wish to thank E. H. Dunn and an anonymous referee for reviewing the manuscript.—JON S. GREENLAW AND RICHARD F. MILLER, Dept. Biology, Long Island Univ., Greenvale, New York 11548. Accepted 15 Dec. 1982.


**Do secondary roosts function as information centers in Black-billed Gulls?**—In a widely-cited hypothesis, Ward and Zahavi (Ibis 115:517-534, 1973) suggested that certain bird assemblages function primarily as information centers, where birds that are unsuccessful in finding food follow more successful birds. Relevant assemblages were said to include breeding colonies, large communal roosts, and "secondary" roosts that sometimes form as satellite aggregations closer to current food sources. Gulls (Larus ridibundus, L. argentatus) were included as examples of species employing secondary roosts, but no one to date appears to have looked closely at gull roosts to see if they could function as information centers. One study (Lowman and Tamm, Am. Nat. 115:285-305, 1980) has examined the relevance of the information center hypothesis at communal roosts of Hooded Crows (Corvus cornix) and Common Ravens (C. corax), but with equivocal results.

Roosts are common on or near foraging areas used by Black-billed Gulls (L. bulleri) breeding inland in New Zealand. These gulls typically feed on short-lived but temporarily rich and patchily distributed food (Evans, Behaviour 79:28-38, 1982) and so might be expected to employ functional information centers as an aid to food finding. I examined this hypothesis for roosts located inland, adjacent to the Ashley River, near Christchurch, in 1979. I found
roosts at 34 separate locations. Thirty roosts lasted no more than 1 day, one lasted up to 2 days, and three lasted up to 3 days, giving a total of 41 site-days of observation.

If an assemblage is to function as an information center, it seems evident (Ward and Zahavi 1973), that it must be located at some distance from current food supplies. In Black-billed Gulls, most roosts were located either on (N = 21 site-days) or immediately adjacent to (N = 13 site-days) the area currently being searched for food. In all of these cases, it appeared to me that the foragers were usually visible to gulls at the roost, and vice versa. Movement between roosts and active foragers was common, often almost incessant, and typically involved direct flights between the two groups. Since the active foragers normally moved about from place to place within sight of the roosts, new recruits from the roost could not have been joining them on the basis of the recruit’s memory of prior feeding spots as required for “leaders” at an information center. Foragers leaving the roost to begin foraging appeared clearly to be cueing directly to the birds already feeding, an example of local enhancement.

At seven other locations, the active foragers eventually moved completely out of sight of the roosting birds. Distances between the roosts and new foraging areas were small (<1 km for five roosts, 1.6 and 2.2 km for the other two), and flights between foragers and roosts continued to occur. These detached roosts were soon abandoned, usually within 1–3 h, in favor of the new foraging area. Because of the short distances involved, it is possible that once the birds from the roosts became airborne they would still have been able to see the foragers. If not, they would almost certainly have known, from their own immediate experience, the correct general direction to fly to regain visual contact with the active foragers.

According to a recent theoretical model developed by Waltz (Am. Nat. 119:73–90, 1982), short distances and ease of locating a new food patch represent resource characteristics that are not conducive to the development of functional information centers.

In conclusion, the tendency for Black-billed Gull roosts to occur on or close to the feeding grounds effectively precludes them from functioning as information centers, at least under the conditions that prevailed on my study area. It remains possible that roosts might function as information centers at other times, e.g., when food is scarce, but there is no evidence for this view. The results of this study and others (Lowman and Tamm 1980; Andersson et al., Behav. Ecol. Sociobiol. 9:199–202, 1981) suggest that the information center hypothesis is not likely to be as general as originally claimed. Some other advantage(s) may underlie the formation of roosts. Several other possible food-related benefits of grouping have been advanced (e.g., Evans, Auk 99:24–30, 1982; Bayer, Auk 99:31–40, 1982), and merit additional examination.

Acknowledgments.—Financial support was received from the Natural Sciences and Engineering Research Council, Ottawa. I thank John Warham for help in New Zealand, and K. Cash, R. Morris, and R. D. Bayer for comments on the manuscript.—ROGER M. EVANS, Dept. Zoology, Univ. Manitoba, Winnipeg, Manitoba R3T 2N2, Canada. Accepted 1 Dec. 1982.


The Rufous-rumped Antwren (Terenura callinota) in Costa Rica.—The Rufous-rumped Antwren (Terenura callinota) has a wide distribution from southern Middle America to Guyana and Perú, but is known chiefly from a handful of specimens from widely scattered localities. The collector Jelski, quoted by Wetmore (Birds of the Republic of Panamá, Pt. 3, Smithsonian Misc. Coll., Vol. 150, 1975), stated that his specimen of the very closely
related Chestnut-shouldered Antwren (T. humeralis) was collected from a wandering flock, moving among the terminal leaves of the branches; virtually nothing else seems to have been published on Terenura spp. antwrens in life. In this note I present the first records of T. callinota from Costa Rica, a northward range extension of ca. 300 km, as well as observations on behavior and annual cycle of this species.

My observations were made at elevations of ca. 1000 m in Parque Nacional Braulio Carrillo, Provincia de San José, on the north slope of the Cordillera Central of Costa Rica. This is an area of heavy sub tropical forest on exceedingly precipitous terrain, with excessively high rainfall; the study area falls in the Premontane Rain Forest life zone of Holdridge (Life Zone Ecology, Tropical Science Center, San José, Costa Rica, 1967). The forest has a broken, irregular canopy reaching heights of 25–35 m; the understory is rather dense, composed chiefly of shrubs (Rubiaceae, Acanthaceae, Gesneriaceae, etc.), small palms, tree-ferns, and large herbs (Heliconiaceae, Marantaceae, etc.). Most of the trees bear heavy epiphyte loads (especially mosses and liverworts, ericads, aroids, cyclothans, orchids, and bromeliads).

The Rufous-rumped Antwren is a very small, slender-billed, long-tailed antwren; in shape, activity, and color pattern it suggests a tyrannulet (e.g., Phylloscoccertes) or a warbler (Parulinae). Indeed, upon seeing my first Terenura I thought I had discovered a new species of flycatcher! The black cap and dusky eyelid of the males are conspicuous, but the diagnostic rufous rump is often covered by the wings; perhaps the best field mark for both sexes is the bright yellow wing-bars. The bird is an active foliage-gleaner, hopping quickly and incessantly about in the leaves and slender twigs at the tips of branches. Sometimes it runs and flits along the twigs, or hangs acrobatically. It plucks prey from both upper and under surfaces of leaves and twigs, or from little tufts of moss, but I have not seen it sally or hover, or rummage in dead leaves or epiphytes as does the Slaty Antwren (Myrmotherula schistiscolor) a frequent foraging companion. Often the bird gives nervous double wing-flicks between foraging maneuvers. Regularly accompanying mixed-species flocks of antwrens, antvireos, furnariids, tanagers (Thraupini), and warblers, pairs or small (family?) groups of T. callinota forage mostly from the upper understory into the lower canopy. Usually silent, the birds will occasionally give an energetic series of squeaky notes, schi schi schi etc., interspersed with softer sputtering or chattering notes. These vocalizations somewhat resemble the more liquid and querulous calls of the furnariid Red-faced Spinetail (Cranioloaerythroops), a frequent attendant species in the same flocks.

I collected two specimens of T. callinota, which are now in the Museo de Zoología, Universidad de Costa Rica. UCR 2364 is an adult female in molt with the ovary not enlarged, taken on 28 September 1980; UCR 2429 is an adult male in fairly fresh plumage with testes moderately enlarged, taken on 14 March 1981. Both birds had the iris dark brown, maxilla black, mandible silver-grey, and tarsi blue-gray; stomach contents of both were small insects (especially beetles and homopterans) and spiders. The weights (7.0 and 7.3 g, respectively) make this the smallest antbird in Costa Rica.

T. callinota is most vocal from about February through May or June, probably the breeding season, as I saw a female gathering nesting material (moss) on 13 March 1981, and a female feeding a full-grown juvenile on 1 July 1981. The annual molt probably occurs mainly in September and October, judging from the female specimen and other molting birds I have seen. The annual cycle of this species thus coincides with those of most other canopy birds of the area for which I have data (Stiles, unpubl.).

That this striking little bird has escaped notice in Costa Rica until now probably reflects several factors. Its habitat is very difficult to work, and the bird seems to occur only in a relatively narrow elevation band (ca. 800–1200 m) that has received little attention from ornithologists because of its inaccessibility. Collectors like C. F. Underwood worked intensively both above and below these elevations in the Cordillera Central, but evidently did not
penetrate the extremely wet and dense forests at about 1000 m on either the Cordillera Central or the Cordillera de Talamanca, along which the distribution of *Terenura* is probably continuous into western Panama.


Radiotelemetry location of nesting Band-tailed Pigeons in Colorado.—Band-tailed Pigeons (*Columba fasciata*) occur throughout many of the forested mountain ranges of western North America (Goodwin, Pigeons and Doves of the World, British Museum [Nat. Hist.], London, England. No. 663. 1967). Most detailed nest information is available for the Coastal race (*C. f. monilis*) in California (Glover, Calif. Fish and Game 39:397–407, 1953; MacGregor and Smith, Calif. Fish and Game 41:315–326, 1955; Peeters, Condor 64:445–470, 1962). Although nests have been reported for the Interior race (*C. f. fasciata*) of Band-tailed Pigeons (Fitzhugh, Literature Review and Bibliography of the Band-tailed Pigeons of Arizona, Colorado, New Mexico, and Utah, Ariz. Game and Fish Dept. Spec. Rept., 1970), no quantitative study of nest-site preference has been attempted due to the difficulty of finding nests. The first two reported nests of *C. fasciata* from Colorado were in the Rampart Range, Pike National Forest (Neff and Niedrach, Condor 48:72–74, 1946; Neff. Habits, Food and Economic Status of the Band-tailed Pigeon. U.S. Dept. Int. Fish and Wildl. Serv. N. Am. Fauna 58. 1947) and few nests have since been reported for the Interior population. The objective of our study was to determine if radiotelemetry equipment could be used to locate nests of Band-tailed Pigeons.

**Study area.**—The study was conducted from mid-May through early July 1981 near Evergreen, Jefferson Co., Colorado. Bandtails were trapped at the Forest Heights site (39°38’N, 105°16’W) at 2146 m elev. (Curtis, M.S. thesis, Colorado State Univ., Fort Collins, Colorado, 1981), where an extensive road network provides reasonable access. Few berry-producing trees or shrubs are found in the area (Braun, Proc. West. Assoc. State Game and Fish Comm. 53:336–344, 1973) and bandtails rely heavily upon grain supplied by local residents. Ponderosa pine (*Pinus ponderosa*) and, at higher elevations, lodgepole pine (*P. contorta*) are the most common overstory trees.

**Methods.**—Cannon nets were used to trap bandtails at Forest Heights (Braun, Methods for Locating, Trapping and Banding Band-tailed Pigeons in Colorado, Colorado Div. Wildl. Spec. Rept. 39, 1976). Captured pigeons were classified as to age and sex on the basis of plumage characteristics (White and Braun, J. Wildl. Manage. 42:564–569, 1978), weighed with a Hanson dietetic platform scale (Drewien et al., J. Wildl. Manage. 30:190–192, 1966), and leg banded.

Radio transmitters were fabricated by the Denver Wildlife Research Center, U.S. Fish and Wildlife Service. Transmitters were powered by an RM 675 mercury battery and had an estimated life of 45 days. An oval-shaped piece of latex rubber was glued to the base of the radio package to provide a bonding surface. Total transmitter weight was 6.3 ± 0.1 g. N = 10 (ca. 2% of pigeon body weight). Feathers on the lower middle back of selected birds were trimmed to about 0.5 cm in length, and the transmitter package was glued to the trimmed area with a cyanoacrylate-base glue.

The receiving system consisted of a portable 12-channel receiver (AVM Instrument Co.,
Table 1


<table>
<thead>
<tr>
<th>Sex</th>
<th>Age</th>
<th>No. of days located (dates)</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>Adult</td>
<td>3 (15–25 May)</td>
<td>Lost contact</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>17 (15 May–12 July)</td>
<td>Located on nest on 6 June</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>16 (15 May–11 July)</td>
<td>Located on nest on 30 May</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>16 (15 May–12 July)</td>
<td>Found radio hanging in tree</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>16 (19 May–11 July)</td>
<td>Located on nest on 10 June</td>
</tr>
<tr>
<td>Females</td>
<td>Adult</td>
<td>6 (15 May–6 June)</td>
<td>Apparent loss to avian predator</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>15 (19 May–11 July)</td>
<td>No nest found</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>16 (15 May–11 July)</td>
<td>No nest found</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>2 (19–20 May)</td>
<td>Lost contact</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>6 (15–24 May)</td>
<td>Lost contact (shot, see text)</td>
</tr>
</tbody>
</table>

Champaign, Illinois), and a 3-element hand-held Yagi directional antenna. Maximum reception range was 18.6 km, although there was considerable variation depending upon topography, vegetation density, and exact pigeon location.

Radio-tagged Band-tailed Pigeons were located throughout the day and attempts were made to find all marked birds at least once weekly from 15 May–12 July. Locations of radio-tagged bandtails were determined by triangulation and direct observation.

Nest locating.—Radio transmitters were placed on four male and three female bandtails on 14 May. An additional male and two females were fitted with transmitters on 18 May. All pigeons had inactive crop glands (indicating they were not yet prepared to feed young) when trapped. Nests of three of five radio-marked males were found but no nests were located for any of the five females (Table 1). Contact was lost with one male and two female pigeons shortly after radio marking.

Radio-marked male Band-tailed Pigeons on nests were easier to locate than females. Males were found on nests from approximately 08:00–17:00 MDT during which time females were at feeding sites. It was necessary to search between 06:00–08:00 and 17:00–20:00 to attempt to find females on nests. Neither time interval was long enough to locate and confirm a nest because extensive hiking was often required to reach nest-sites near rugged mountain peaks. Late afternoon electrical and rain storms also hampered efforts to find nesting females.

The area within 30 km of the trap site was searched intensively at least once weekly for all radio-marked birds. Considering the maximum reception range of 18.6 km, radio-marked pigeons not located may have flown a considerable distance from Forest Heights. Contact was lost with a female 9 days after radio marking. This pigeon was shot on 2 September near Montrose, Colorado; approximately 240 km from the trap site, with the transmitter still attached. Radio loss or failure may also explain the difficulty in finding certain pigeons.

Nest and habitat description.—Due to the small sample size, it was not possible to identify factors important in nest-site selection. The three bandtail nests located were in lodgepole pines along sloping (40–80%) ridgetops. A nest found by Neff (1947) in the Rampart Range was also in a lodgepole pine along a steep ridge.

Glover (1953) reported an outside nest diameter of 19.8 cm for eight nests in California. Nest heights in his study ranged from 2.1–45.7 m and the distance from the bolé ranged...
Table 2

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Value</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest size, L × W (cm)</td>
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<td>22–27 × 19–26</td>
</tr>
<tr>
<td>Nest depth (cm)</td>
<td>8.8</td>
<td>7.8–9.5</td>
</tr>
<tr>
<td>Bowl depth (mm)</td>
<td>28</td>
<td>25–30</td>
</tr>
<tr>
<td>Distance from trunk (cm)</td>
<td>56</td>
<td>0–109</td>
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<tr>
<td>Diameter of twigs of nest (mm)</td>
<td>3.2</td>
<td>2.9–3.7</td>
</tr>
<tr>
<td>Twig length (mm)</td>
<td>—</td>
<td>200–300</td>
</tr>
<tr>
<td>Nest height (m)</td>
<td>4.6</td>
<td>2.1–5.9</td>
</tr>
<tr>
<td>Tree DBH (mm)</td>
<td>245</td>
<td>160–374</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2845</td>
<td>2719–2938</td>
</tr>
<tr>
<td>Distance from trap site (km)</td>
<td>10.9</td>
<td>7.1–14.0</td>
</tr>
</tbody>
</table>

from 0.3–1.8 m. MacGregor and Smith (1955) reported an average nest height of 11 m (range = 3.7–29.0 m) for 26 nests. Peeters (1962) found six of 11 nests between 4.6 and 6.1 m in height. All nests in his study ranged from 2.1–12.2 m above the ground. These data for nests of pigeons in the Coastal population were similar to those for the three nests that we observed (Table 2).

Stand composition at nest-sites varied from 65–100% lodgepole pine and the understory vegetation consisted of sparse blueberry (Vaccinium spp.), pinegrass (Blepharoneuron spp.), russet buffaloberry (Shepherdia canadensis), quaking aspen (Populus tremuloides), common juniper (Juniperus communis), and bearberry manzanita (Arctostaphylos uva-ursi). Rock cover ranged from a few stone-size rocks to 15–20% stones and boulders. The parent material at all three nest-sites was granitic. The aspect of slopes where nests were found varied from NNE to S (AZ 20–175°). Nest limbs faced NNE to ESE (AZ 20–100°).

Nests of Band-tailed Pigeons can best be described as a loose platform of twigs that contain little besides the squabs. A few shell fragments were noted in two nests. One to three breast feathers were also found in two of three nests. Initially, chick droppings were found in only one nest, but as the squabs matured the accumulation of droppings became more apparent in all nests.

Radio-telemetry equipment was a useful tool for locating nests of Band-tailed Pigeons in Colorado. Females on nests were not found during this study. Because both male and female bandtails share nesting activities, it is doubtful that nest preference data would differ between nests located by following one or the other sex. Because males are associated with nests during a large proportion of the daylight hours, it may be more efficient to place radio transmitters only on this sex. Aerial radiotracking combined with a ground crew in vehicles and on foot, should aid in finding nests and birds for which radio signals have been lost.

Acknowledgments.—Financial assistance was provided by the Accelerated Research Program for Migratory Shore and Upland Game Birds and the Colorado Division of Wildlife. Federal Aid in Wildlife Restoration Project W–88–R. We thank P. Hegdal and J. Bourassa for loan of equipment and technical advice, and K. Giesen for assistance in collecting nest data. J. A. White and M. Stromberg reviewed an early draft of the manuscript.—PAUL D. CURTIS, Dept. Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, Colorado 80523 and CLAIT E. BRAUN, Colorado Division of Wildlife, Wildlife Research Center, 317 W. Prospect, Fort Collins, Colorado 80526. Accepted 15 Dec. 1982.
Breeding of a mixed pair of white-shielded and red-shielded American Coots in Michigan.—American Coots (*Fulica americana*) and Caribbean Coots (*F. caribaea*), the latter a problematic species, are mainly allopatric. American Coots breed throughout most of North and Andean South America, and the latter form breeds entirely in the Antilles and locally in northwestern Venezuela and Trinidad. American Coots from North America winter south into the Antilles, and it is unknown whether they breed sympatrically with the Caribbean Coots in the Caribbean or whether Caribbean Coots are a color morph of the widespread American Coot (Ripley, Rails of the World, David R. Godine, Boston, Massachusetts, 1977; Blake, Manual of Neotropical Birds, Vol. 1, Univ. Chicago Press, Chicago, Illinois, 1977; Bond, Twentieth and Twenty-second Supplements to the Check-list of Birds of the West Indies [1956], Acad. Nat. Sci. Philadelphia, 1976, 1980). In the absence of information on the reproductive behavior of the two forms in the same locality, systematists have conservatively and tentatively listed the two as distinct species. In recent years, Caribbean Coots have been reported in Florida (Bolte, Am. Birds 28:734–735, 1974; Eldson, Florida Nat. 48: 25, 1975), in Tennessee (Hall, Am. Birds 36:177, 1982), and in Michigan (Powell, Jack-Pine Warbler 60:126, 1982).

A white-shielded coot was first noted by Alan Ryff (pers. comm.) in the marsh by the nature trail in Metrobeach Metropark near the shore of Lake St. Clair, Macomb Co., Michigan, on 20 April 1982. The bird had an all-white bill with a maroon ring near the tip, but lacked a red callus, typical of shields of American Coots in North America. The swollen frontal shield was textured with grooves and pits and was broad at the base (Fig. 1) and was slightly yellowish in color in subtle contrast to the distal white portion of the bill. In the field and in color photographs we noted a narrow (2–3 mm wide) band of red or reddish-brown at the base of the shield not at the site of the callus in the typical local *F. americana*. In plumage the bird resembled other local coots and had white under tail coverts, and in flight the whitish tips of the secondaries were revealed. This set of plumage characters applies both to North American and Caribbean coots (Voous, Studies on the Fauna of Curacao and other Caribbean Islands, Vol. 7, Martinus Nijhoff, The Hague, The Netherlands, 1957).

We observed the white-shielded coot over several weeks and determined that it was mated with a red-shielded American Coot. On 24 April the white-shielded bird fought in a territorial skirmish with a neighboring red-shielded coot, and it repeatedly carried nest material as it flew to a nest-site in the marsh. On 26 April it copulated with a red-shielded coot (the white-shielded bird was on the top, so was a male), and on 2 May it patrolled a territory of about 40 × 50 m in the open cattail marsh. On 18 May we photographed a red-shielded bird incubating at least four eggs in the nest in the center of the territory still controlled by the white-shielded bird, at the site where it had flown down into the marsh with nesting material. On 29 May the white-shielded coot and a red-shielded coot were observed over an hour 10–15 m from the nest with both adults attending and feeding at least three newly-hatched, downy coot young, each no larger than about 80 mm. The nest was empty except for one addled egg, and the center was dry in early morning when the cattails around it were wet with dew, suggesting that the young were brooded on the nest the night before. Neighboring coot territories were searched to compare the timing of nesting in other coots in the local population. One territory had a brood of eight young of similar size to the first brood, and another had a nest with 10 warm eggs. All local coots except the apparent male in the local territory had a red callus on the frontal shield.

We saw that the white-shielded coot was aggressive and territorial, it was accepted by a local female as a mate early in the local breeding season, it was successful in breeding, and it provided parental care to the young. Female American Coots in North America apparently
Fig. 1. A white-shielded American Coot (frontal [top] and side [bottom] views) at Metrobeach Metropark, Macomb Co., Michigan, on 2 May 1982.
do not require their mates to have red frontal shields, and red-shielded males respect the territories of a male lacking this signal character.

Coots in Andean populations of *F. americana* vary with some birds having a red callus on the shield and others lacking it (Gill, Condor 66:209–211, 1964). In one population Gill found six mated pairs with one member having a white shield and the other a red shield; some of these mixed pairs had young. Prior to this field observation the two forms of coots were considered distinct species; they now appear to be a single species (and subspecies, *F. a. ardesiaca*). Gill suggested that the red-shielded and white-shielded coots of the West Indies (the former considered inseparable from North American *F. a. americana* by Bond [1976] and Ripley [1977], and the latter being the “Caribbean Coot”) might be conspecific as well. Apparently the white-shielded individuals resembling those more common in the Antilles rarely occur also as breeding birds in North America. Florida observations of “Caribbean Coots” may have been of northern wintering coots insofar as the white-shielded birds in Florida are seen in winter but not in the northern breeding season when the wintering migrants have departed (Stevenson, Am. Birds 30:709, 1976; 36:288, 1982; LeGrand, Am. Birds 33:170, 1979).

The shield of American Coots varies by swelling in the breeding season, remaining large while the birds hold breeding territories and are paired, then regressing to a more flattened condition after territorial and breeding behavior has ceased. Experimental implants of testosterone result in growth of the shield, and shield size varies with testis size in wild coots (Gullion, Wilson Bull. 63:157–166, 1951). Gullion (1951:163) noted that “no two birds have identically the same callus shape.” Thus, the callus and shield are developmentally labile within a bird and also vary among birds. While the individual variability and seasonal development suggest that variation in the shield of coots is not due simply to a genetic dimorphism, a dimorphism may be involved. Whatever the developmental explanation of differences in coots, the observations and experiments document a considerable variation in the shields of American Coots.

Populations of coots in North America, in the Caribbean, and in parts of South America may have different frequencies of red- and white-shielded birds. A white-shielded bird at Tallahassee, Florida, formed a pair bond with a red-shielded bird and behaved aggressively towards other coots (Stevenson, Am. Birds 36:288, 1982). White-shielded coots were not widely reported in North America before they were illustrated as a “species” in a popular field guide (Peterson, A Field Guide to the Birds, 4th ed., Houghton Mifflin, Boston, Massachusetts, 1980), and the form may have been overlooked. However, coots with “all white” and coots with some “yellow” and no dark on the shield have been seen near Arcada, Los Angeles Co., and at San Francisco, Marin Co., California (Luis F. Baptista, in litt.), so the form may be rare but widespread in North America. Censuses of the different morphs in natural populations are needed.

Observations of the white-shielded coot in Michigan do not confirm that the bird was Caribbean in origin nor do they establish that Caribbean Coots are morphs of the American Coot within the Caribbean. The fact that white- and red-shielded coots in populations in eastern North America and in Andean South America interbreed successfully and behave as a single species do point, however, in that direction for coots in the Caribbean.

Acknowledgments.—For comments on the manuscript we thank L. F. Baptista and H. M. Stevenson. Robin Payne helped search for the coot nests.—ROBERT B. PAYNE, Mus. Zoology, Univ. Michigan, Ann Arbor, Michigan 48109; and LAWRENCE L. MASTER, Michigan Natural Features Inventory, Box 30028, Lansing, Michigan 48909. (Present address LL.M: Eastern Regional Heritage Program, The Nature Conservancy, 294 Washington St., Boston, Massachusetts 02108.) Accepted 23 Nov. 1982.
Tree Swallow pairs raise two broods in a season.—Although Tree Swallows (*Tachycineta bicolor*) are normally single-brooded, Wetherbee (Bird-Banding 4:160, 1933) recorded one instance in Connecticut of a female laying a second clutch after raising one young from a first brood. The second attempt, however, was unsuccessful. Chapman (Bird-Banding 26: 45–70, 1955) mentioned one pair which had two broods in a season (the only case in 22 years) but gave no other details. Weydemeyer (Bird-Lore 36:100–105, 1934) stated that second broods occurred in Montana, but gave no evidence that marked pairs had been followed. Here I report on two pairs of Tree Swallows which raised two broods in a single season.

Nest boxes suitable for Tree Swallows have been maintained by the Long Point Bird Observatory at two sites near Port Rowan, Haldimand-Norfolk Regional Municipality, Ontario: the Backus Conservation Area (B) and the Sewage Lagoons (S), since 1975 and 1977, respectively. The boxes are on metal poles spaced at 24-m intervals in lines or grids. The S site has an exceptionally abundant food supply of flying insects (mainly Chironomidae), while the B site usually has a smaller food supply (unpubl.). During the breeding season, boxes are checked frequently, often daily, and contents recorded. After the eggs hatch, adults are trapped and banded at the nest. Females and males are sexed by presence of a brood patch or cloacal protuberance, respectively.

In 1979 one pair raised a brood in box S20, then moved to box S19 (24 m distant) and raised a second brood. On 11 May there was a complete nest in box S20 and the first egg was laid on 14 May. Eggs were laid daily until a clutch of six was completed on 19 May. The eggs hatched between 31 May and 2 June. On 12 June female A and male B were trapped as they visited the box to feed the young (swallows designated by capital letters refer to banded individuals verified by trapping). Female A had been banded as an adult at the same box in 1978. The brood of six in 1979 was banded on 13 June and left the nest between 18 and 22 June. At least one of the banded young is known to have survived the post-fledging period as it was captured as a breeding female in 1980 and 1981.

Meanwhile, box S19 had been occupied by another pair (female C and male D, trapped on 3 June) whose first egg had been laid on 13 May and last young of four fledged on 18 June. The nest was empty on 24 June, but it contained four eggs on 28 June and a clutch of six was completed on 30 June. Five eggs hatched, two by 12 July, three others by 14 July. Female A was trapped at box S19 on 16 July and again, with food in her bill, on 18 July, when male B was also trapped there. No other adults were in attendance. Five young were banded on 25 July when they averaged 12 days old. Their mean weight of 19.8 g (range = 18.5–21.4 g) was 3 g lower than that of the first brood at the same age (mean 22.8 g, range = 21.9–24.6 g). On 29 July (age 16 days) two were dead and the other three were underweight, one chronically (14.0, 17.5, and 18.1 g compared with 20.9–22.1 g for six young in the first brood at 16 days), and all were heavily parasitized by *Protocalliphora* larvae. Thus, three young were raised to at least 16 days of age. Whether or not they all fledged successfully is uncertain, as the box was not checked again until 1 September, but there was then no evidence of additional mortality. Neither the young nor the adults were found again in subsequent years.

In 1982 a pair raised two broods in box B43. The first egg was laid on 7 May, the earliest laying date ever recorded in either the S or B areas and 3 days earlier than in any other 1982 nest. Eggs were laid daily until a clutch of six was completed on 12 May. The eggs hatched 25–26 May and female E was captured on the nest on 26 May. She had been banded as an adult at the same box in 1981. Male F was captured in B43 on 4 June 1982. One of the young died between 6 and 7 June, but the others fledged in good condition between 12 and 17 June.

Adult swallows were noted exhibiting territorial behavior in the vicinity of B43 on several
dates until 29 June when one new egg was present. A clutch of four was completed probably on 3 July (no egg was laid on 1 July). Two eggs had hatched by 16 July and the other two were piped. Male F was captured in the box with four young on 30 July. On 31 July female E was captured as she carried food to the nest box. This second brood was also underweight; they averaged 19.1 g (range = 17.6–20.0 g) at 14 days compared with a first brood average, interpolated from 12 and 16 day weights, of 23.4 g (range = 21.6–24.4 g). Nevertheless they fledged successfully between 3 and 7 August. Female E and male F had both started post-nuptial molt of the primaries when captured.

To raise two broods instead of one a pair of birds must lengthen its breeding season by starting earlier or ending later. Time can be gained by reducing the period of parental care (Blancher and Robertson, Wilson Bull. 94:212–213, 1982) or the between-brood interval. The 1979 double-brooded pair was among the earliest breeders that year and the 1982 pair was the earliest ever recorded. Most of the time gained for raising second broods, however, resulted from an extension of the end of the season. Unfledged young of first broods are rarely found at this locality after the first week of July.

Blancher and Robertson (1982) provide evidence (but see Peck, Wilson Bull., in press) that a pair of another normally single-brooded species, the Eastern Kingbird (Tyrannus tyrannus), attempted to raise a second brood. They (1982:213) suggest that the “decision whether or not to start a second brood immediately after the first brood fledges should be governed by the probability of rearing young from the second brood compared to the probability of decreasing the first brood’s chances of survival.” This relationship is unlikely to be important in the Tree Swallow, in which there appears to be little post-fledging parental care. Moreover, the relative fitnesses of the single-brooded and double-brooded strategies depend not only upon the success of first and second broods and interactions between them, as suggested by Blancher and Robertson (1982), but also upon the effects of the two strategies on parental survival and probability of future reproductive output. The rarity of second broods in Tree Swallows is most likely governed primarily by the net effect on fitness of the probability of success of second broods and the probability of reduced future reproduction. An abundant food supply and an early season may be factors which could tip this balance in favor of second broods and may have influenced the pairs reported here. In the Cliff Swallow (Hirundo pyrrhonota) the incidence of second broods apparently varies between years (Samuel, Wilson Bull. 83:284–301, 1971), so possibly this species has evolved the ability to assess whether the one- or two-brood strategy is likely to be more favorable under a given set of conditions. Brown and Bitterbaum (Wilson Bull. 92:452–457, 1980) suggest that second broods in Purple Martins (Progne subis) may be limited both by greater mortality of the young and by conflicting energetic requirements of parents who raise second broods while starting the postnuptial molt. Low weights of young Tree Swallows in second broods and concurrent flight feather molt in their parents lend support to these ideas. Similar selective factors may operate on late broods in birds which are normally single-brooded (Hussell, Ecolog. Monogr. 42:317–364, 1972), presumably indicating that in these species second broods would be, for the same reasons, even less adaptive than late first broods.

Acknowledgments.—Thanks to the following for assistance with the fieldwork: A. Chetwynd, P. Christgau, B. Kubicki, A. Lambert, K. Lambert, D. Luckert, M. Palmer, D. Plummer, T. Quinney, B. Silieff, R. Smith, M. Smith, B. Woodford. Thanks also to C. R. Brown and G. L. Holroyd for their comments on the manuscript. Long Point Region Conservation Authority and Ontario Ministry of Environment permitted use of the sites and Long Point Bird Observatory provided financial support.—DAVID J. T. HUSSELL, Long Point Bird Observatory, P.O. Box 160, Port Rowan, Ontario N0E 1M0, Canada. (Present address: Wildlife Research Section, Ontario Ministry of Natural Resources, P.O. Box 50, Maple, Ontario L0J 1E0, Canada.) Accepted 5 Mar. 1983.
Male "incubation" in a Chestnut-collared Longspur.—During 1981, 16 breeding pairs of Chestnut-collared Longspurs (Calcarius ornatus) were studied in Grand Forks County, North Dakota. Females were mist-netted and banded with federal and colored leg bands. Daily activity observations and nest checks were made in each territory and time budgets were conducted for males. Although the "typical" male behavior during incubation involves use of perches in the general vicinity of the nest (Bailey and Niedrach, Wilson Bull. 50:243–246, 1938; Harris, Wilson Bull. 56:105–115, 1944), the males in this study were found to differ greatly in their temporal and spatial attendance to nests. Two males occasionally "stood guard" on the ground near the nest, and one male, #14, was observed "incubating" on four different occasions.

This is the first record of incubation behavior by a male for this species. The nest in territory 14 was located during the construction phase and a four-egg clutch was completed on 31 May. During egg-laying and incubation the male was frequently observed on three perches within 4.2 m of the nest. On 3 June, at 11:09, the male circled low over the nest and vocalized. When the female left the nest the male landed and began incubating. His position was observed from a distance of 3.6 m with binoculars until 11:19. At 11:22 the female returned and replaced the male on the nest. On 4 June, the male was flushed from the nest and the female was found foraging 7.2 m away. On 5 June, at 11:29, the male was again observed on the nest, being replaced by the female at 11:34. A similar exchange of positions was witnessed on 6 June at 10:30.—Ann M. Wyckoff, Dept. Biology, Univ. North Dakota, Grand Forks, North Dakota 58202. Accepted 30 Nov. 1982.


Study area and methods.—The study was carried out at the Lower Souris National Wildlife Refuge (now called the J. Clark Salyer National Wildlife Refuge) in north-central North Dakota in May, June, and July of 1965 and 1966. Wilson’s Phalaropes bred on the freshwater marsh in the floodplain of the Souris River, about 4.8 km E of Upham, McHenry Co. The predominant vegetation was cordgrass ( Spartina pectinata ) interspersed with small and large patches of squirreltail ( Hordeum jubatum ), whitetop ( Schlochloa festucacea ), and phragmites ( Phragmites communis ) (see Murray 1969, for photographs of the study area). My observations were made as opportunity permitted and concerned mainly nesting biology.

Arrival.—Wilson’s Phalaropes were already present by 8 May when I arrived in 1965. In 1966 I arrived on 30 April and saw the first phalaropes on 3 May (a group of one male and four females and another of two females). On 4 May I found one group of two males and three females. One male and female kept close company, feeding and resting together, and were generally undisturbed by other phalaropes (they were once approached by a female, which was chased away by the female). On 6 May the group numbered three males and eight females. Two of the males were each accompanied by a single female, whereas the third male was accompanied by four females, one of which seemed to dominate the others.

Although these observations are few and the population small, some birds did give the
appearance of being paired on arrival or, more likely, immediately after arrival (Jehl, Auk 85:515-520, 1968). One cannot be certain, however, that these pairings were permanent (at least through egg-laying) without marked individuals. These and other counts, taken hap-hazardly, indicate that females outnumbered males from the time of arrival until they left the marsh entirely: at least, I saw no indication of an abundance of males in almost daily, all-day visits to the marsh.

Nests.—Wilson's Phalaropes at Lower Souris built substantial nests of dead stems from surrounding grasses. The height above the ground of 11 nests ranged from 2-7 cm ($\bar{x}$ = 5.0), and the outside diameter of these nests measured from 9-13 cm ($\bar{x}$ = 11.3). These may have been similar to those seen by Kumlien (cited by Nelson, Bull. Nuttall Ornithol. Club 2:38-43, 1877), who thought that the nests of Wilson's Phalaropes resembled those of the Red-winged Blackbird (Agelaius phoeniceus). One nest (not measured because I could not find it after the birds had left) was a cup of grasses in a Spartina tussock. The nests at Lower Souris, then, were different from those in eastern North Dakota (Howe 1975b) and Alberta (Höhn 1967), which were more similar to those of the Red Phalarope (Phalaropus fulicarius) (Höhn, Ibis 113:335-348, 1971; Mayfield, Living Bird 17:7-39, 1978) and Red-necked Phalarope (Phalaropus lobatus) (Höhn, Auk 85:316-317, 1968), which consisted of little more than a grass-lined scrape. Indeed, the first eggs were often laid on the bare ground (Höhn, 1967, 1968; Howe 1975b; Mayfield 1978), with the lining added afterward. Perhaps the Wilson's Phalaropes at Lower Souris built such substantial nests because of the extreme wetness of the substrate.

Laying.—I found eight clutches before they were completed. Seven provided one instance and one provided two instances for which the date of laying of single eggs could be determined. Eggs were laid on consecutive days except at nest 1965-6, in which laying was interrupted by a snowstorm, and at nest 1965-1, in which the third egg was extraordinarily large. A more precise time of laying could be determined for four eggs: between 11:40 and 11:50, 11:45 and 15:40, 13:50 and 15:00, and 09:30 and 17:00.

The earliest eggs were laid on 15 May and the latest on about 7 June. Thus, the laying season on my study area spanned a little more than 3 weeks.

Clutch-size.—Of the 26 completed clutches, 25 contained four eggs, and one contained three. The latter was clutch 1965-1, in which the third egg was the unusually large one mentioned above. One incomplete clutch of two eggs was interrupted by the death of the male, whose carcass was found near the nest.

Incubation.—Not unexpectedly, males performed virtually all the incubation. However, as did Höhn (1967), I once recorded a female leaving a nest containing a completed clutch of eggs, but whereas Höhn believed his record may have resulted from a slip of his pen, I am not convinced that I was mistaken.

I was able to determine the incubation period, from the laying of the last egg to the hatching of the last egg, for three clutches. These incubation times were 20, 21, and 23 days. The latter period may have been caused by a snowstorm occurring during incubation. Following the storm I checked the five nests then under observation and found no incubating birds and cold eggs. By the early afternoon, however, the males had returned, and the eggs were warm. At least one clutch hatched, and two were later taken by predators.

Reproductive success.—In 1965, 22 of 65 eggs in 17 nests hatched, six did not hatch, nine were lost to predators, two did not hatch because the male died, and the fate of 26 was unknown (I did not keep track of them). In 1966, 15 of 40 eggs in 10 nests hatched, six did not hatch, nine were lost to predators, and the fate of nine was unknown. Thus, considering only the eggs followed, 37 of 70 (53%) hatched in the 2 years of the study.

Role of the female.—In 1965 I found females in attendance at all but one nest throughout the major portion of the incubation period. They appeared to serve as lookouts, flying up and toward me as I approached the nest, sometimes from as far away as 50 m. Often a small
group of females would form, joined shortly by the males. In order to find a nest I had to ignore the first bird to flush in an area and mark the position of the second bird to flush.

One female and a male approached me on 19 June, 5 days after the first young hatched at the nest I was inspecting. Not all the females associated with nests stayed as long. I first noticed a decline in the number of females on 18 June, and by 23 June I could find no females on the marsh. Several left while males were still incubating eggs.

Although one cannot be certain without marked birds, these observations suggest that males and females may remain paired for a lengthy period. Because these observations seemed unusual I intended to study the females more closely in 1966. In 1966, however, the females laid their eggs and immediately departed. I was able to find phalarope nests more easily because the males allowed me a closer approach before flushing, and I was not distracted by having to distinguish males from females. I chose to avoid known nest-sites as much as possible in order to reduce disturbance to the mateless males. As a result I hardly saw a phalarope after egg-laying.

Höhn (1967) stated that the females leave long before the eggs hatch, but Höhn (1967) and Johns (1969) mentioned females joining males in alarm flight or males with chicks, respectively. Only Nelson (1877:42-43) seems to describe the behavior that was so prevalent on my study area in 1965: “Incubation is attended to by the male alone. The female, however, keeps near, and is quick to give the alarm upon the approach of danger. The females are frequently found at this time in small parties of six or eight; and should their breeding ground be approached, exhibit great anxiety, coming from every part of the marsh to meet the intruder, and, hovering over his head, utter a weak nasal note, which can be heard only a short distance.” Nelson (1877) also remarked upon the sudden disappearance of females (although this occurred in mid-July in Illinois rather than in late June, as I observed in North Dakota).

One other investigator has reported similar experiences with phalaropes. Concerning the Red-necked Phalarope in Labrador, Newfoundland, Austin (Mem. Nuttall Ornithol. Club 7, 1932:107) wrote, “Though I spent in all about three hours on the island in company with the male and the young, the female never put in an appearance, which is the only time that has happened to me. Whenever, elsewhere, I have found the birds obviously breeding, both parents eventually appeared, though the male was usually the first on the scene, and was always the more excited.”

What seem unusual about my observations in 1965 and those of Nelson (1877) and Austin (1932) are the proportion of females attending males and the length of time the females remained in attendance. Other observations indicate fewer females attending males and briefer periods of attendance. Howe (1975b) noted two female Wilson’s Phalaropes remaining near their nest-sites for 2 days after the clutches of four eggs were completed. In the Red Phalarope at Bathurst Island, Mayfield (1978) observed a female defending her mate 5 days after he found the completed clutch, although normally the pair bond ended quickly. In Siberia, also, Kistchinski (Ibis 117:285–301, 1975) noted that pair bonds ended quickly, with the males driving the females away. In Spitzbergen, however, Ridley (Ibis 122:210–226, 1980) observed males chasing female intruders rather than their mates, and pair bonds lasted 1–14 days after egg-laying. In Alaska, pair bonds lasted 1–13 days after the clutch was completed with the female remaining near the nest (Schamel and Tracy, Bird-Banding 48:314–324, 1977). Schamel and Tracy (1977) suggested that the variable pair bond allowed the females to obtain new mates when additional males were available.

In the Red-necked Phalarope in Alaska, Höhn (1968) noted that both parents were present at one of the two nests that produced young (total nests = 11) and responded to the presence of an observer, but in Finland, Hildén and Vuolanto (Ornis Fennica 49:57–85, 1972) thought that those females accompanying newly hatched broods were interested in the males rather than in the chicks.
The pair bonding behavior in phalaropes seems variable and open to several interpretations. This suggests the need for further study, especially with color-marked individuals.

Polyandry in phalaropes.—Although the phalaropes represent the classic example of reversed sexual dimorphism in size and coloration and were long suspected of having polyandrous mating relationships, these have been demonstrated only recently in the Red-necked Phalarope (Raner, Fauna och Flora 67:135–138, 1972; Hilden and Vuolanto 1972) and Red Phalarope (Schamel and Tracy 1977) but not at all in Wilson’s Phalarope, even though this species shows the greatest sexual dimorphism in the group. Höhn (1967), Johns (1969), Howe (1975a), and I (this study) found that female Wilson’s Phalaropes outnumbered males early in the season during pair-formation and egg-laying, giving little opportunity for polyandry to occur. Only Kagarise (1979) found males available for second matings of females, but these were males from failed nests in a population that suffered extraordinarily high rates of predation on the eggs.

The desertion of mates may be advantageous when the deserters have opportunities to obtain additional mates (Pienkowski and Greenwood, Biol. J. Linnean Soc. 12:85–94, 1979), but in phalaropes such opportunities seem limited, males being in excess only occasionally in the Red-necked Phalarope (Hilden and Vuolanto 1972) and Red Phalarope (Schamel and Tracy 1977) and seemingly only rarely in Wilson’s Phalarope. Because polyandrous species often have high losses of eggs compared with other shorebirds, it may be tempting to suggest that males are often available as potential mates for deserting females. However, the mates of deserting females also suffer high losses, and, thus, a female does not necessarily increase her reproduction by changing mates for her second clutch. Indeed, one can at least hypothesize that in a species with high egg loss, females could increase their probability of successful reproduction by remaining with their mates, not only laying replacement clutches but even providing protection or other assistance in reducing the probability of egg loss. Whether females stay with their mates or desert them would depend upon the probability of having two or more males tending successful clutches. It can be shown (Murray, unpubl.) that this probability is greater when the sex ratio favors males than when first clutches suffer a high loss of eggs. Thus, high egg loss seems an inadequate explanation for desertion of nests by females.

Female Wilson’s Phalaropes seem able either to stay with their mates or to desert them. What they do undoubtedly depends upon particular conditions, which are at present unknown. What is known about phalaropes is that males only rarely exceed females in number and that polyandry is infrequent in the populations that have so far been studied. One can only wonder what selective forces have led to the striking reversed sexual dimorphism of these species.

Acknowledgments.—I thank E. O. Höhn and H. F. Mayfield for corresponding with me about aspects of their work on phalaropes, M. Gochfeld for references, and J. R. Jehl, Jr., and the reviewers, M. A. Howe and E. H. Miller, for reading, commenting upon, and improving the manuscript. My work in North Dakota was supported by the Frank M. Chapman Memorial Fund of the American Museum of Natural History.—BERTRAM G. MURRAY, JR., Dept. Biological Sciences, Livingston Coll., Rutgers Univ., New Brunswick, New Jersey 08903. Accepted 12 Mar. 1983.


Nest-site selection by Eastern Kingbirds in a burned forest. —Unlike many species of North American tyrantids, Eastern Kingbirds (Tyrannus tyrannus) use a variety of habitats for breeding (Bent, U.S. Natl. Mus. Bull. 179, 1942). In seral and riparian communities, nests are generally concealed in the foliage of woody vegetation, but in habitats where
arboreal sites are lacking, kingbirds may select atypical nesting sites that offer little or no concealment (Roberts, The Birds of Minnesota, Univ. Minn. Press, Minneapolis, Minnesota, 1932; Baust et al., Bull. Entomol. Soc. Am. 27:23–25, 1981).

Following fire, species richness and densities of some birds may decrease, but Niemi (Loon 50:73–84, 1978) found that kingbirds remained common despite a decrease in habitat complexity. Because a crown fire will reduce the number of potential nesting sites, these birds must be opportunistic in selecting nest-sites in order to reproduce successfully in burned habitats.

From 1977–1980, data were collected on nest-sites of Eastern Kingbirds in a burned jackpine (Pinus banksiana)-northern pin oak (Quercus ellipsoidalis) forest in northern Clare County, Michigan. Observations were limited to a 20-ha plot burned by wildfire in mid-April 1977. Neither ground nor crown vegetation survived the fire, but subterranean rhizomes of perennial forbs and some shrubs eventually regenerated, forming a mosaic ground cover over much of the area.

The post-fire landscape consisted largely of standing burned jackpines interspersed with pin oak "shrubs," produced by secondary growth at the bases of charred trees. Regeneration by jackpine was minimal, probably due to severe drought conditions during 1977. The unburned forest surrounding the study site consisted principally of a closed canopy of jackpines and pin oaks. Although kingbirds did not occur in the unburned forest, they have nested repeatedly on the burn where the number of breeding birds has remained relatively unchanged (Table 1). Presumably, the species was absent from the area prior to the fire.

Nearly 65% of the nests were constructed in charred trunks containing cupped depressions that were formed by embers that burned into heartwood. The remaining nests were placed among burned branches of jackpines. Three nests that occurred in cupped depressions were reused during consecutive years, suggesting that birds return to previous nest-sites. Fairfield (Long Pt. Bird Obs. Ann. Rept. 13, 1972) found that color-marked kingbirds returned to the same nest-sites. One nest that was used consecutively failed during 1978 when it was deserted after a prolonged period of rain (Hamas, Jack-pine Warbler 57:26–27, 1979). The nest-site was not used again until 1980. Hildén (Ann. Zool. Fenn. 2:53–75, 1965) indicated that site tenacity may be reinforced by learning in several species of birds, but at sites where nesting has been unsuccessful during a previous year, birds are less likely to return.

Although data on clutch-size and hatching success were incomplete for kingbirds using the burn, young fledged from all nests. The lack of concealment by foliage, an important determinant of nesting success in kingbirds (Murphy, Condor, in press), did not contribute to predation. Thus, reproductive success in local or isolated habitats may favor continued use of atypical nest-sites and ultimately lead to behavioral variation in species that are habitat generalists.

| Table 1 | USE OF NESTING SITES BY EASTERN KINGBIRDS IN A BURNED FOREST |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Number of nests | 3               | 4               | 3               | 4               | 14              |
| Nest-site       |                 |                 |                 |                 |                 |
| Burned branches | 2               | 1               | 0               | 2               | 5               |
| Trunk depressions| 1               | 3               | 3               | 2               | 9               |


Herring Gull males eat their own eggs.—Although Herring Gull (Larus argentatus) adults are known to eat their own chick offspring (Parsons, Ph.D. thesis, Univ. Durham, Durham, England, 1971) we know of no documented observations of them eating their own eggs. On two occasions we observed male Herring Gulls break open and eat eggs in the clutches they were incubating: on 12 May 1978 at a colony on Fighting Island, Detroit River (near Lasalle, Essex Co., Ontario, Canada) and on 22 May 1979 at the Lighthouse colony near Port Colborne, Ontario, Niagara Co., Canada. The sex of the birds in question was determined by observations of copulation together with size differences (male larger) within the pair. Both members of the pair at the Lighthouse colony were individually color-banded. Both pairs laid three-egg clutches. The clutch at Fighting Island was completed on 26 April 1978 and was one of the earliest of all clutches (N = 40) in the colony. The clutch at the Lighthouse was completed on 6 May 1979, during the “peak” of clutch initiation (N = 75) at the colony. Thus, in both instances the behavior was observed 16 days after clutch completion.

Details of the two observations follow. At Fighting Island, an elevated blind was located about 15 m from the nest of interest. The male was incubating at the beginning of the observation period (08:20) and although the female was present intermittently throughout the day, the male was not relieved by her during observations of the nest (completed 18:30). At 16:50 the male, apparently unalarmed, stood over the clutch. With active pecking movements the bird then broke open one of the eggs and consumed the contents. He resumed incubation of the remaining eggs at 16:55. The female was present during the egg-eating episode. Both eggs hatched from the clutch and one chick eventually fledged.

At the Lighthouse colony, an elevated blind was located about 10 m from the nest of interest. The male had incubated the clutch for at least 2 h (14:00–16:00) when he stood over the clutch, broke open all three eggs within 30 sec and then partially ate the contents. His mate, present during the event, had attended the male at the nest-site during the previous hour. She had been trapped that morning (22 May 1979) and radio-transmitter equipment attached to her back. The pair remained at the nest-site throughout the breeding season although no further eggs were laid. Both clutches had been checked daily from clutch initiation. All eggs in the Fighting Island clutch were intact 24 h before the incident occurred, while at the Lighthouse all eggs were intact on the morning of the incident.

In evolutionary terms, egg-eating behavior is clearly maladaptive as considerable time and energy have already been invested with relatively little subsequent investment needed to bring the eggs to term. Eaten eggs may be inviable through infertility or embryo mortality; however, detection of the appropriate egg by an adult seems unlikely. Although the age of the birds in each pair was unknown, all were in adult plumage when the incidents occurred and the early laying dates suggest older, experienced birds (Chabrzyk and Coulson, J. Anim. Ecol. 45:187–203, 1976). Thus, we rule out the possibility that the anomalous egg-eating behavior was a result of youth or inexperience of the males. An obvious proximate explanation is that our activity in both colonies was sufficiently disturbing to cause the aberrant behavior by these two individuals. Certainly in the case of the trapping activity at the Lighthouse colony, this would be reasonable. However, over 40 adult Herring Gulls have been trapped at this colony between 1978–1980 and there is no evidence that either this procedure or the
attached radio-transmitter equipment had any negative effect on the adults, their clutches
or chicks (Morris and Black, J. Field Ornith. 51:110–118, 1980; Morris et al., J. Field Ornith.
52:242–244, 1981). Birds at both colonies were aware of observers in the blinds but always
settled down and exhibited normal incubation and chick feeding behavior a few minutes
after entry of the blind by the observer. Despite the apparent lack of negative effects of
trapping and harnessing procedures, the act of egg eating at the Lighthouse was most likely
a result of these disturbances. An alternative explanation, possibly applicable to the Fighting
Island observation, is that an incubating adult unattended for long periods by its mate eventu-
ally experiences simultaneous drives to incubate and to leave the nest. The resulting
displacement activity is egg eating. These observations may explain some incidences of egg
disappearance noted by several workers at gull colonies (e.g., Gilbertson, Can. Field-Nat.

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organizations and individuals.—John W. Charidine and Ralph D. Morris, Dept. Biologi-
cal Sciences, Brock Univ., St. Catharines, Ontario L2S 3A1, Canada. Accepted 3 Feb. 1983.


Opportunistic feeding on whale fat by Wilson’s Storm-Petrels in the western
North Atlantic.—Species of Procellariiformes have often been observed feeding on the
(Auk 94:385–386, 1977) collected a Fork-tailed Storm-Petrel (Oceanodroma furcata) at Nelson
Lagoon, Alaska, that was feeding on decayed fat from a stranded gray whale (Eschrichtius
robustus). Although anecdotal information is available, our observations provide the first
positive documentation of feeding on whale fat for procellariids in the western North Atlantic.

On 11 July 1978, while we were surveying the pelagic distributions of marine birds from
Cape Hatteras to Nova Scotia, a recently killed fin whale (Balaenoptera physalus) was seen
at 41°10'N, 68°48'W. No birds were seen with the carcass at this time. Three days later, the
carcass was resighted in a bloated condition. Blue sharks (Prionace glauca) were seen eating
its flesh and approximately 400 Wilson’s Storm-Petrels (Oceanites oceanicus) were feeding
on floating bits of carrion around the whale. On 24 August 1979, several hundred Wilson’s
Storm-Petrels were seen feeding on pieces of decayed fatty tissue from the carcass of a dead
fin whale at 41°48'N, 67°55'W. Two of these birds were collected and their proventriculi
contained whale fat. Except for a skua (Catharacta sp.), which was seen in the vicinity of
the latter sighting, no other birds were associated with these carcasses. In view of this limited
evidence that Wilson’s Storm-Petrels and other procellariids may on occasion be associated
with and selectively feed upon the fatty tissue of dead cetaceans, we feel it appropriate to
identify possible reasons for this opportunistic feeding behavior.

Recent evidence indicates that procellariids use the sense of smell to find food. The size-
ratio of the olfactory bulb to cerebral hemisphere is high in procellariids and suggests an
found that procellariids are able to determine odor trails at night as well as in daylight.
Controlled observations by Hutchinson and Wenzel (Condor 82:314–319, 1980) also supported
the view that procellariids use olfaction to locate food. Since foraging by smell is based on
the ability to follow an airborne odor-gradient (Wenzel, pp. 41–64 in Behavior of Marine Animals, Vol. 4, Burger et al., eds., Plenum Press, New York, New York, 1980), it follows that a decaying whale would provide a strong stimulus as a potential food item.

Ashmole and Ashmole (Peabody Mus. Nat. Hist., Yale Univ. Bull. 24:1–131, 1967) suggested that it is disadvantageous for procellariformes to transport intact food containing a large percentage of water. By digesting food as it is caught and then excreting the excess water, these birds can build up large food reserves. Dermal whale tissue in whales has a low ratio of water relative to fat content (Arai and Sakai, Sci. Repts. Whale Res. Inst. 7:51–67, 1952); such food can be converted to stomach oil quickly and carried with a minimum demand for water excretion. Thus, we suggest that decaying whale fat, which is detectable by smell and is easily digestible with a high caloric value, would be a most desirable food item when available to procellariids at sea.

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Enhanced foraging efficiency in Forster’s Terns.—Light winds have been considered to be detrimental to the feeding efficiency (i.e., no. of successful prey captures/no. of attempts for prey) of Great Blue Herons (Ardea herodius) (Bovino and Burtt, Auk 96:628–630, 1979), but apparently have no effect on Common Murre (Uria aalge) foraging (Birkhead, Br. Birds 69:490–492, 1976). Grubb found no direct wind effects on Osprey (Pandion haliaetus) feeding efficiency, although he did find a reduction in efficiency due to rippling of the water surface (Grubb, Auk 94:146–149, 1977). However, for Common Terns (Sterna hirundo) and Sandwich Terns (S. sandvicensis) Dunn (Nature 244:520–521, 1973) found that a mild wind and rippling water increased feeding-success rates. We studied the effects of mild wind, water surface condition, and direction of tidal flow on feeding efficiency of Forster’s Terns (S. forsteri).

A total of 212 min of observation were made primarily between 06:00 and 11:00. Data were collected from 4–23 August 1980. The study-site was a bridge over a causeway leading from the mainland to Chincoteague Island, Accomak Co., Virginia (75.5°W, 38°N). Eighty-two individual observations of Forster’s Terns were made. For each individual the feeding method used was recorded, as was the total number of dives for fish and the number of captures. Wind speed was estimated every 30 min using a Beaufort wind scale (BWS). Also, direction of tidal flow and water surface condition (i.e., height of waves: smooth, 1 cm, 2 cm, etc.) were recorded for the same interval.

Terns were considered to be actively foraging when the head and bill were oriented downward (Salt and Willard, Ecology 52:989–998, 1971), and this method was used for both styles of foraging. A description of perching behavior may be found in Reed et al. (Wilson Bull. 94:567–569, 1982). Terns dived from a height of approximately 4–6 m. Only actively foraging terns were included in the analysis.

Efficiency comparisons for Forster’s Terns were made between individuals feeding under no-wind (BWS 0) and mild (BWS 1 and 2) wind conditions using a contingency χ² test. The same test was used to compare successes/h and attempts/h of foraging. Because the feeding efficiency of Forster’s Terns varies significantly with feeding strategy (i.e., aerial vs perched
Table 1
Comparisons of Attempts/h and Captures/h for Prey by Forster’s Terns
Between Winds of Different Speeds

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>df</th>
<th>Attr./h</th>
<th>χ²</th>
<th>Succ./h</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerial</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>BWS 0 (no-wind)</td>
<td>15</td>
<td>28</td>
<td>79.8</td>
<td>8.6a</td>
<td>20.4</td>
<td>0.036</td>
</tr>
<tr>
<td>BWS 1 and 2 (mild)</td>
<td>14</td>
<td>46.8</td>
<td></td>
<td></td>
<td>19.2</td>
<td></td>
</tr>
<tr>
<td>Perched</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BWS 0</td>
<td>22</td>
<td>52</td>
<td>68.4</td>
<td>0.01</td>
<td>25.8</td>
<td>2.91</td>
</tr>
<tr>
<td>BWS 1 and 2</td>
<td>31</td>
<td>67.2</td>
<td></td>
<td></td>
<td>39.6</td>
<td></td>
</tr>
</tbody>
</table>

*a P < 0.005.

attack (Reed et al., 1982), each strategy was analyzed separately. Effect of tidal direction
was calculated using a Student’s t-test.

Wind speed and water surface condition were highly correlated during this study (r = 0.87, P ≤ 0.01), and their individual effects could not be statistically separated. Direction
of tidal flow was found to have a non-significant effect on success rate (r = −0.57, P > 0.05). This is in accord with previous findings (Dunn, J. Anim. Ecol. 44:743–754, 1975; Erwin, Ecology 58:389–397, 1977).

Forster’s Terns showed a significant increase in foraging efficiency while aerial-feeding
from no-wind (25.4%) to mild wind (40.6%) (χ² = 5.22, df = 1, P ≤ 0.05) but not when
feeding from a perch—no-wind (45.2%) and mild wind (58.8%) (χ² = 3.71, df = 1, P > 0.05).

The data on number of attempts/h and successes/h for aerially feeding Forster’s Terns
showed that significantly more attempts were made by individuals feeding during no-wind
conditions than by individuals feeding during mild wind conditions (χ² = 8.6, df = 28, P ≤ 0.005) (Table 1). However, there was no significant increase in capture rate (no. of prey items
taken/h) (χ² = 0.036, df = 28, P > 0.05). Perched feeders showed no significant change in
dive rate (χ² = 0.01, df = 52, P > 0.05) or success rate (χ² = 2.91, df = 52, P > 0.05) whether
feeding under no-wind or mild wind conditions.

Dunn (1973) proposed two explanations for the increase in feeding success with light wind
that she observed: (1) with a mild wind terns need not flap so vigorously while hovering,
which might therefore reduce the chance of being detected by their prey, and (2) the rippling
of water may actually impede the prey’s vision. We would predict perch-feeders to show
no wind-enhanced increase in feeding efficiency if detection by prey was the key since
perched feeders are not visible to the fish (Reed et al., 1982). No significant change in the
feeding efficiency of perched birds was observed (χ² = 2.91, df = 52, P > 0.05). This suggests
that water surface condition, more than wind speed, is the most important factor in the
increased efficiency. The noted increase in efficiency by aerial feeders possibly reflects
an improvement in aerodynamic stability and diving speed. If reduced flapping resulted in
an increased efficiency (Dunn’s [1973] first hypothesis), we would have expected an increased
capture rate in aerial feeders, and this did not occur (Table 1). It should be noted that the
increased efficiency is due to a decrease in attempts/h, not an increase in successes/h. The
reduced number of attempts may be due to reduced visibility of prey (Salt and Willard 1971; Grubb 1977). The success rate remains constant, probably because the fish’s vision is more
hindered than is the tern’s (Dunn 1973), and evasive actions by the prey are thus less
effective. This notion is supported by the reduced visibility of aerial feeders during mild wind.

Both of Dunn’s (1973) explanations of increased success rate are based on the prey’s ability to detect foraging terns. Our results support her second hypothesis (as stated above) that water surface conditions are the most important factor influencing foraging efficiency in terns due to its inhibitory effect on the prey’s ability to detect terns.

This study was paid for by a grant from the Millersville State College Alumni Association.—J. MICHAEL REED AND SAMUEL J. HA, Dept. Biology, Millersville State College, Millersville, Pennsylvania 17551. (Present address JMR: Dept. Zoology, Univ. Montana, Missoula, Montana 59812.) Accepted 21 Feb. 1983.


Atypically colored Little Blue Heron eggs.—Egg colors of the Little Blue Heron (Egretta caerulea) are described as pale hues of blue, green, and bluish green (Bent, U.S. Natl. Mus. Bull. 135, 1926; Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962; Oberholser, The Bird Life of Texas, Vol. 1, Univ. Texas Press, Austin, Texas, 1974; Hancock and Elliott, The Herons of the World, Harper and Row, Publ., New York, 1978). In 1973, I examined 2332 Little Blue Heron clutches in Texas and found two clutches of which the eggs had a ground color of deep olive-buff (Ridgway, Ridgway Color Standards and Nomenclature, Washington, D.C., 1912) with very small brownish orange spots (Kornerup and Wanscher, Reinhold Color Atlas, Reinhold Publ. Corp., New York, New York, 1962) less than 0.5 mm in diameter each scattered over the entire shell, but more concentrated near the large end. One clutch was in the Ennis heronry (Ellis County, 32°20’N, 96°37’W) and the other clutch was in “The Slough” heronry at the Beaver Catfish Hunting and Fishing Club (Anderson County, 31°52’N, 95°53’W). The two heronries were about 100 km apart. Exact locations and descriptions of these heronries can be found in Telfair (pp. 88–90, 96–99, 109–117, 130–133 in Ph.D. diss., Texas A&M Univ., College Station, Texas, 1979).

To my knowledge, no eggs of this olive-buff color have been reported in the literature nor have I noted any others among several hundred clutches I have seen since 1973. Answers to my inquiries about 28 museum egg collections confirmed the uniqueness of my observations. However, one clutch (taken in Orange Lake, Florida) in the Reading Public Museum and Art Gallery (Pennsylvania) has olive-buff blotches; seven clutches in the New York State Museum (taken in Florida and South Carolina) have a wash of extremely pale, inconspicuous olive blotches or stains, while some have a few small and very widely scattered orange spots; four clutches at the Museum of Zoology, University of Michigan (all taken in Texas) have brownish splotches and smears; one clutch in the Baylor University Strecker Museum (Waco, Texas) has small orange spots; and several eggs in the Corpus Christi Museum (Texas) have very small brownish orange spots. Thus, based upon my observations, literature descriptions, and museum collections, absence of green and blue pigment in the egg shells of the Little Blue Heron occurs in less than 0.1% of clutches.

All five eggs in the Ennis clutch produced “normal” chicks and the pipped egg shells were collected. One of the four eggs in “The Slough” heronry was collected; but the others were destroyed in a flood. Both clutches were photographed (35 mm Kodachrome 64 color transparencies) and each egg was measured. Length and breadth for each of the nine eggs were within the range of measurements obtained from 180 randomly chosen eggs from the two heronries.

Perhaps these atypically colored eggs resulted from a rare allele that may be restricted to
Texas: and since the two clutches were in heronries not far apart (100 km) possibly the two females were related (Charles G. Sibley, pers. comm.). Olive-buff colored eggs are much less conspicuous in nests than are normally colored eggs and, perhaps, would be less subject to predation by sight-oriented predators. I suggest that other persons interested in ardeid eggs may find atypically colored eggs for other species. If so a study of the significance of atypical egg coloration among ardeids could be undertaken.


Eye-color changes in Barrow’s Goldeneye and Common Goldeneye ducklings.—At hatching, the irides of Barrow’s Goldeneye (Bucephala islandica) and Common Goldeneye (Bucephala clangula americana) ducklings may be brown, gray-brown, gray, or even blue-gray; irides of adults of both species are yellow, irides of juveniles are brown (Palmer, ed., Handbook of North American Birds, Vol. 3, Yale Univ. Press, New Haven, Connecticut, 1976). Given the close relationship of brown colors to yellow, one might expect the transition from natal to adult iris color to proceed in a simple sequence such as: gray-brown, brown, light brown, brownish yellow, yellow. This is not the case. In 1964, casual observation of half-grown ducklings of each species, which I had earlier examined as day-old young, disclosed a seemingly unusual eye-color: an intense ultramarine blue. The color, apparently undescribed in any waterfowl species, seemed equally unrelated to the natal gray-brown, the juvenile brown described in the literature, and the adult yellow. Each duckling had also a dark, brownish ring around the pupil, evidently similar to the brown "Innenring" noted by Bauer and Glutz von Blotzheim (Handbuch der Vögel Mitteleuropas, Vol. 3. Akademische Verlagsgesellschaft, Frankfurt am Main, 1969) in eyes of juvenile B. c. clangula females. The purpose of this note is to describe the appearance and development of the two eye-color components in known-age ducklings of both goldeneye species. Note: It is not known whether the blue eye-color appears in half-grown young of the congeneric Bufflehead (Bucephala albeola). Presumably, the detection of a lighter transitional color in this species would be made more difficult by the large amount of dark pigment in the irides of both hatchlings and adults; the natal iris color is dark brown or dark gray-brown, the adult iris is "dark brownish" (Palmer 1976).
Fig. 1. Changes in hue and chroma of the first color component (natal color) of the irides of Barrow's Goldeneye ducklings. The duration of the appearance of each hue in the developmental eye-color sequence is indicated by a horizontal line parallel to the time line. For example, in Fig. 1, hue 2.5PB was continuously present in one or more Barrow's ducklings from day 3–day 6, and again from day 34 until the end of the study. Note that in Figs. 1 and 2, the solid horizontal lines refer to hues displayed by both sexes; elsewhere, solid lines indicated hues or chromas of males, dotted lines those of females.

Methods.—In 1976, while conducting a morphometric study of Barrow's and Common goldeneye ducklings at the Delta Waterfowl Research Station, I made regular measurements of the eye-color of each species as the ducklings grew. Measurements were taken outdoors in north daylight, using first the Atlas de los Colores (Villalobos-Dominguez and Villalobos, El Ateneo, Buenos Aires, 1947) and later, the Munsell Soil Color Charts (Munsell Color Company, Baltimore, Maryland, 1973), with the addition of charts 5PB and 7.5PB. Matte samples from the Munsell Book of Color (Munsell Color Company, Baltimore, Maryland, 1929) were used to evaluate colors not contained in the augmented soils collection. Color attributes measured were hue (e.g., purple-blue [PB], blue [B], yellow-red [YR]), value (e.g., dark [2/3], light [6/7]), and chroma (e.g., dull [1/2], bright [8], brilliant [12]). Color notations used in this note follow the Munsell system; a synonymy of these colors with three other color systems is provided in the Appendix.
Sixteen Barrow’s and 15 Common goldeneyes, representing two broods of each species, were hatched in incubators from wild-gathered eggs. At approximately 24 h of age, they were numbered, sexed by cloacal examination, and placed in rearing pens, where they were undisturbed except during the few hours required for measurements. I observed the Barrow’s ducklings over a period of 65 days (and again at 5 months of age, without a color standard) and the Common Goldeneye ducklings during their first 7 weeks of life. Color measurements were taken daily for the first 10 days and twice weekly thereafter. Only first-day data were used from four Barrow’s and five Common goldeneye ducklings that died during the study. Although the remaining 22 individuals were examined on every measuring day, the age difference of 1–3 days among individuals within a brood meant that the sample size for any given day of age was often small, averaging 2.2 for Common Goldeneye males, 3.9 for Barrow’s males, and 2.6 for females of both species.

Results and discussion.—All 31 goldeneye ducklings had gray-brown or dark gray-brown irides at hatching. The blue eye-color appeared (time of first appearance, day 3–day 20) in all individuals of both species, replacing the natal colors, and became, successively, purple-blue, blue, and green-blue. As well, M. Jackson (pers. comm.) confirmed the existence of blue eye-color in half-grown wild Barrow’s Goldeneye ducklings on her study area in British Columbia. W. R. Miller (pers. comm.) observed blue eyes in wild Common Goldeneye duck-
ling's in Vermont, and C. J. Guiget noted "iris blue" on the label of a young male Barrow's duckling (BCPM 14393, ca. 10 days old) that he collected in 1940 near Barkerville, British Columbia. The brownish ring around the pupil appeared a few days after hatching.

Changes in the hue and chroma of the first component, the natal color, were most marked (Figs. 1, 2). As early as the third day of life, certain individuals of both species displayed traces of gray (N) or dull purple-blue (5PB, 7.5 PB) at the periphery of the iris. The color remained, increasing in area (some individuals) and rising to a peak of brilliance (Munsell /12) on day 26 in a Common Goldeneye male and more rapidly, on day 12, in two Barrow's males. Irides of two Common Goldeneye males sustained a brilliance of /10 until day 46; irides of one Barrow's male remained at /12 until day 34. Although individual color differences in both sexes were obvious, chroma in the irides of females of both species appeared to increase more slowly, and to reach a lower level of brilliance than in those of males. At about 5 weeks of age, in a few individuals of both species (two males, one female), the hue of the irides began to appear less purple, more blue (2.5PB), the chroma to decrease slightly, and the value, heretofore medium (4/ or 5/), to measure 6/. By 8 weeks of age, the iris hue of three Barrow's Goldeneyes (two males, one female) was 10B 8/4 (a pale, rather dull blue), and at 65 days, the hue of the three birds' irides measured 2.5B 8/4—a clear, pale turquoise blue.

In the 10 Barrow's ducklings examined at 5 months of age, irides of the six males were all some tint of clear, pale green-yellow, with little or no cloudy light brown area around the pupils. Eye-colors of the four females were less uniform: irides of three were various tints of light, dull green-yellow with irregular areas of cloudy golden brown, but the irides of the fourth were quite gray, with a cloudy light brownish area around the pupils.

Changes in the brown component of the iris color were less dramatic (Figs. 3, 4).
FIG. 4. Changes in hue, chroma, and area of the second color component (brown ring) of the irides of Common Goldeneye ducklings.

dark ring contrasted well with the lighter natal colors (gray, gray-brown, blue-gray), but poorly with the darker ones (dark gray-brown, brown). It was evaluated initially as a dark (2.5/ to 3/), very dull (0.5 to /1.5) orange-brown (5YR), which became somewhat yellower (7.5YR, 10YR) and lighter (3.5/ to 4/) at about 6 weeks in a few males of both species. The brown iris-rings of the females did not turn lighter and yellower, but remained dark orange-brown (5YR), although the chroma in nearly all ducklings of both species increased to /3 or /4 by 7 weeks.

The rapid increase in area of the brown color paralleled almost exactly the increase in brilliance of the blue color in both species. At times, the brown color seemed to take on a purplish hue of its own, although this proved to be an illusion. Repeated color evaluations produced no evidence of a true purple tint. The area of brown iris increased more rapidly in Barrow’s than in Common goldeneye ducklings and, after about 5 weeks, seemed larger in females of both species than in males. Once enlarged, the size of the area remained more or less stable throughout the study, although there were small, irregular size fluctuations in individual birds. It is not surprising that the blue color should have gone undescribed until now, as it is most often reduced to a narrow rim on a predominantly brown iris, and as such, is quite inconspicuous.

Acknowledgments.—I am grateful to R. Trethewey and P. Ould for supplying live goldeneye ducklings; to the Canadian Wildlife Service for collection and possession permits; to the Delta Waterfowl Research Station for hatching, rearing, and laboratory facilities; and to the British Columbia Provincial Museum for loaning specimens. I thank the University of Manitoba Libraries (P. Anthony, R. Bennett) for extended loans of the Ridgway and Villalobos color standards, L. Forster for her help in preparing the Ridgway-Munsell reference index, and K. Parkes, B. Batt, and H. Ouellet for reading the manuscript and for making useful sug-
gestions. Finally I am grateful to my husband, C. Nelson, who drew Figs. 1–4 and provided essential transportation facilities. The research was funded in part by a grant from the Explorations Program of the Canada Council.—COLLEEN HELGESON NELSON, Manitoba Museum of Man and Nature, 190 Rupert Avenue, Winnipeg, Manitoba R3B 0N2, Canada. Accepted 22 Feb. 1983.

APPENDIX
A Synonymy of Representative Eye-colors of Goldeneye Ducklings in Four Color Notation Systems

<table>
<thead>
<tr>
<th>Munsell</th>
<th>Villalobos</th>
<th>Ridgway</th>
<th>Smithe</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Blues and Neutrals</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5 PB 4/1</td>
<td>(N/UUC) 7–1°</td>
<td>LII [BLUE] Dark Plumbeous 87—Medium Plumbeous</td>
<td></td>
</tr>
<tr>
<td>5PB 3.5/1</td>
<td>U–5–1°</td>
<td>LIII [CG] Blackish Slate × Slate Color 78—Plumbeous</td>
<td></td>
</tr>
<tr>
<td>7.5PB 4/1</td>
<td>UUV–5 (1°/2°)</td>
<td>XLIX [V–B] Violet-Slate 73—Indigo</td>
<td></td>
</tr>
<tr>
<td>5PB 4/4</td>
<td>(UUC/U) 6–6°</td>
<td>XLII [BG–B] Deep Delft Blue</td>
<td></td>
</tr>
<tr>
<td>7.5PB 5/6</td>
<td>(U/UUV) 8–7°</td>
<td>XXIV [V–B] Grayish Violet-Blue</td>
<td></td>
</tr>
<tr>
<td>7.5PB 5/8</td>
<td>(U/UUV) 8 (9°/10°)</td>
<td>XXIV [V–B] Dull Violet-Blue</td>
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</tr>
<tr>
<td>7.5PB 4/12</td>
<td>U–6 (11°/12°)</td>
<td>XXI [BV–B] Diva Blue 170A—Ultra-marine Blue</td>
<td></td>
</tr>
<tr>
<td>7.5PB 5/12</td>
<td>U–8–13°</td>
<td>XXI [V–B] Cornflower Blue</td>
<td></td>
</tr>
<tr>
<td>*2.5PB 7/8</td>
<td>(CCU/C) 15–12°</td>
<td>VIII [G–BB] Pale Methyl Blue</td>
<td></td>
</tr>
<tr>
<td>*10B 8/4</td>
<td>(C/CU) 16–10°</td>
<td>VIII [BG–B] Pale Blue (Ethyl Blue) × XX [BG–B] Persian Sky Blue</td>
<td></td>
</tr>
<tr>
<td>*7.5PB 8/4</td>
<td>C (16/17) 8°</td>
<td>VIII [G–BB] Pallid Methyl Blue × XX [BG–B] Persian Blue</td>
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### APPENDIX
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<table>
<thead>
<tr>
<th>Munsell</th>
<th>Villalobos</th>
<th>Ridgway</th>
<th>Smithe</th>
</tr>
</thead>
<tbody>
<tr>
<td>5YR 3/1</td>
<td>(SSO/SO) 3–2°</td>
<td>XLVI [OY–O] Fuscous Black</td>
<td>21—Fuscous or</td>
</tr>
<tr>
<td></td>
<td>(natal color)</td>
<td></td>
<td>121—Van Dyke Brown</td>
</tr>
<tr>
<td>5YR 4/1</td>
<td>OOS (6/7) (1°/2°)</td>
<td>XLVI [OY–O] Fuscous ×</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(natal color)</td>
<td>XLV [OR–O] Dusky Drab</td>
<td></td>
</tr>
<tr>
<td>*7.5YR 3/4</td>
<td>(SO/OOS) 4–4°</td>
<td>XXIX [OY–O] Verona</td>
<td>121A—Prout’s</td>
</tr>
</tbody>
</table>

* Most Ridgway equivalents of the Munsell notations were taken from an unpublished reference index prepared by the author and a second observer, using the augmented Munsell Soil Color Charts (1973), the Munsell Book of Color, matte samples (1929), and a good copy of Color Standards and Color Nomenclature (R. Ridgway, by the author, Washington, 1912). Villalobos equivalents and synonymies of starred (*) notations were prepared by the author alone. All synonymies were made either in north daylight or under 7500K lamps in the booth described by Nelson (Wilson Bulletin 94:225–229, 1982). Synonymies made by other observers under the same or other conditions may be expected to differ slightly from those presented here. Components of Munsell and Villalobos colors are listed by hue, value, and chroma in that order; the Ridgway notation is represented only by plate number, verbal name, and hue components in brackets [1]. Intermediate Villalobos and Ridgway equivalents are expressed in this way: 5YR 4/1 = OOS (6/7) (1°/2°) = XLVI [OY–O] Fuscous × XLV [OR–O] Dusky Drab; near-equivalents selected by the author from the Naturalist’s Color Guide, Pt. 1 (Smithe, Am. Mus. Nat. Hist., New York, New York, 1975 and 1981), are listed by number and name. The order of the notations approximates that of their appearance in the developmental eye-color sequence.


**Unusual bathing behavior of the Fork-tailed Flycatcher in Colombia.**—On 8 March 1978, while conducting a crocodile (*Crocodilus* sp.) census along the Tomo River, Vichada, Colombia, I observed Fork-tailed Flycatchers (*Tyrannus savana*) engaged in unusual group behavior. Six birds were perched 10 m up in a dead tree at water’s edge on the south bank of the river. The birds were flying in an ellipsoidal pattern from the perch-site to the water, hovering briefly, and immersing themselves, in turn, before returning to the tree.

In 75 days on the Tomo River I saw both Fork-tailed Flycatchers and Tropical Kingbirds (*Tyrannus melancholicus*) using a similar flight routine to drink from the river. However, in each instance only the beak touched the water in an attenuated skimming motion. My observations of the Fork-tailed Flycatchers were made from 10 m and I saw no food or water taken and no skimming behavior. The site of entry into the water was approximately the same for each bird.

The Social Flycatcher (*Myiozetetes similis*) has been reported to occasionally enter water up to thigh depth to capture tadpoles, and also to perch above deeper water, flying down to
seize floating objects from the surface without entering the water (Skutch, Pacific Coast Avifauna 34:428, 1960). The Rusty-margined Flycatcher (*Myioborus cayanensis*) has been known to fly low over the water during rainstorms (Rylander, *Wilson Bull.* 84:344, 1972), but the flight pattern was parallel to the water surface and swallow-like in nature.

In Surinam, Haverschmidt (Birds of Surinam, Livingston Pub. Co., Wynnewood, Pennsylvania, 1968:311) saw Great Kiskadees (*Pitangus sulphuratus*) taking small fish by diving like a kingfisher, and bathing in the same manner. The Fork-tailed Flycatchers were possibly engaged in bathing, although only minimal preening was noted. My observation was made at mid-afternoon of a hot (>35°C) day during the dry season. No breeze was detectable and the water surface was calm. Given the above, the possibility that the birds were attempting to cool themselves cannot be discounted.

My presence in Vichada was funded by the Estación de Biología Tropical Roberto Franco, Villavicencio, Colombia, and the Smithsonian Peace Corps Environmental Program.—William W. Lamar, Dept. Biology, Univ. Texas at Arlington, Arlington, Texas 76019. Accepted 1 Feb. 1983.


**Probable investigator-induced egg drop by a Horned Lark.**—Dump nesting, community nests, and egg dropping are widely reported in the literature (Edminster, American Game Birds of Field and Forest: their Habits, Ecology, and Management, Scribner, New York, New York, 1954; Heusmann, J. Wildl. Manage. 36:620–624, 1972; Weeks, *Wilson Bull.* 92:258–260, 1980). Explanations for these occurrences generally hypothesize a lack of proper timing or a disruption in the nesting cycle such as loss of the nest. Given the opportunity, females of some species will seek a substitute nest after the loss of their own; however, if the laying cycle is at a critical stage the egg may be dropped indiscriminantly. Once an egg follicle reaches a certain point in development reabsorption is no longer possible and laying must take place. Thus, a Wood Duck (*Aix sponsa*) which intended to lay in the nest of a conspecific but was suddenly repulsed from the nest box, had to deposit an egg in open water (Clawson et al., J. Wildl. Manage. 43:347–355, 1979).

Horned Larks (*Eremophila alpestris*) are noted for their stealth about nest-sites and their aversion to revealing the location of a nest. Pickwell (Bent, U.S. Natl. Mus. Bull. 179, 1942) termed the manner in which Horned Larks quietly leave a nest well in advance of impending danger as “casual abandonment.” Several investigators have reported the reluctance of brooding females to return to a nest while a threat persists in the vicinity (Sutton, *Wilson Bull.* 34:131–141, 1927; Garrett, M.S. thesis, Ohio State Univ., Columbus, Ohio, 1948; Beason and Franks, *Auk* 91:65–74, 1974; Wackenhut, M.S. thesis, West Virginia Univ., Morgantown, West Virginia, 1980).

In late spring of 1979, while studying a population of Horned Larks on reclaimed surface mines in Preston County, West Virginia, an egg drop was observed. On 30 May a female Horned Lark was seen carrying nest material. The bird never approached a nest but a search of the area revealed a freshly scraped depression, possibly the beginning of a nest. Subsequent monitoring indicated no further use of the site although two males and a female were regularly seen in the area. On 4 June an observer was positioned in the vicinity to find what was then assumed would be an active nest. Once the female was located she was watched through binoculars. While openly watching from a distance of 20 m, the observer (KS) saw the bird settle in a 2 m² patch of bare earth and remain stationary for approximately 15 min. When the bird resumed activity the area where she had settled was searched and a freshly laid egg was discovered in the exact position the female had occupied. There was no sign
of nest construction in the area. On 5 June the egg lay in the same place with nothing changed except that a small hole had been poked in the shell. On 11 June an active nest containing three eggs was found within 30 m of the spot where the egg had been dropped. When the nest was rechecked on 13 June all eggs were gone; determination of the nest chronology was not possible. Therefore, it could not be verified that this nest was active when the egg was dropped. However, assuming a nest was completed within a few days of when the female was seen carrying nesting material, this nest would have been active at that time. The clutch would have been complete by about 5 June, and hatching would have occurred about 15 June.

We believe that a normal, undisturbed nest existed in the vicinity of the dropped egg, probably the nest which was located on 11 June. When the egg was dropped, the observer was positioned directly between the female and the nest which was subsequently found. It seems likely that the female was inhibited from approaching even for the purpose of depositing an egg. To our knowledge this is the first reported incidence of a Horned Lark dropping an egg or of any species dropping an egg due to voluntary nest avoidance.

The selective advantage of abnormal egg deposition remains unclear, but given the circumstances here the strategy employed by this Horned Lark seems beneficial. In that predation accounts for such a great loss among ground nesting species (in this study 70% of eggs and nestlings produced was lost to predation) any way of avoiding nest betrayal is likely to be advantageous.—P. B. WACKENHUT, 105 Conneaut Lake Rd., Greenville, Pennsylvania 16425; KENNETH A. STRAIT, 302 Emmans St., Flanders, New Jersey 07836; AND ROBERT C. WHITMORE, Division of Forestry, West Virginia Univ., Morgantown, West Virginia 26506. Accepted 12 Jan. 1983.


Red-bellied Woodpecker responses to accipiters.—While studying Red-bellied Woodpeckers (Melanerpes carolinus) at Archbold Biological Station, 13 km S of Lake Placid, Highlands Co., Florida, I saw three hawk attacks on this species. The first occurred in an open grove of citrus and other exotic trees; the others were in xeric pine-oak woodlands.

At 15:07 on 11 December 1981, I heard a Red-bellied Woodpecker giving “scream” calls. When I approached, I saw an immature Sharp-shinned Hawk (Accipiter striatus) flying 4–5 m above the ground, clasping the woodpecker’s legs in its talons. Three sec later the birds broke contact and the woodpecker flew to the nearest tree. Until their separation the woodpecker screamed continuously. When first heard the calls seemed to originate at ground level, suggesting that the birds were not airborne. MacRoberts and MacRoberts (Ornithol. Monogr. 21, 1976) heard an Acorn Woodpecker (M. formicivorus) give “scream” calls continuously when it was caught by a Cooper’s Hawk (A. cooperii).

A “scream” call is also given by Red-bellied, Red-headed (M. erythrocephalus), Pileated (Dryocopus pileatus), and Hairy (Picoides villosus) woodpeckers, Yellow-shafted Flickers (= Northern Flickers) (Colaptes auratus) (Norris and Stamm, Bird-Banding 36:83–88, 1965), and Acorn Woodpeckers (MacRoberts and MacRoberts 1976) when handled during banding. A typical sound spectrograph (Kay Electric Company Sonagraph, wide band-pass filter) of the vocalizations recorded (Sony Cassette-Corder TCM-121) while banding an adult female Red-bellied Woodpecker is shown in Fig. 1. While banding, I was mobbed by Scrub Jays (Aphelocoma coerulescens) in apparent response to the “scream” calls, but mobbing behavior was not employed by nearby conspecifics.

On 16 December 1981 at 13:32, a male and female Red-bellied Woodpecker were perched in trees about 25 m apart when I observed a third Red-bellied Woodpecker about 75 m away
Fig. 1. Sound spectrograph of typical “scream” calls given by a Red-bellied Woodpecker while being banded.

flying in an erratic manner and giving rapid, agitated *cla* calls (Kilham, Wilson Bull. 73: 237-254, 1961) before disappearing into the understory. Seconds later, a Sharp-shinned Hawk flew from the understory near this bird. It appeared that the woodpecker had eluded capture through evasive flight before reaching the dense undergrowth. The hawk headed toward the pair. As it approached, the birds hitched to the underside of their perches where they remained motionless as the hawk flew overhead and out of sight. Both birds then returned to their former positions.

On 14 April 1982 at 07:07, I watched a male Red-bellied Woodpecker enter a nest cavity as his mate flew to it, pursued by a female Cooper’s Hawk. The female woodpecker landed momentarily at the cavity entrance, scrambled to the opposite side of the trunk, then flew erratically toward the dense understory while uttering agitated *cla* calls before disappearing quietly into the vegetation. The hawk gave up the chase when the woodpecker disappeared, flew to a nearby tree, perched 10 sec, then flew from sight. The female woodpecker was next observed 18 min later giving *kwir* calls (Kilham 1961) from a nearby tree.

Kilham (Wilson Bull. 86:35-42, 1974) reported erratic flight by red-bellies and other woodpecker species in the apparent absence of predators. He predicted aerial predator avoidance through erratic flight and suggested that his observations represented play-training for future events. My observations confirm his prediction.

Acknowledgments.—I thank L. L. Short, L. Kilham, J. N. Layne, and G. E. Woolfenden for their helpful comments. Fieldwork was supported by a New York State University Fellowship and a grant from the Chapman Memorial Fund of the American Museum of Natural History.—LILIAN J. SAUL, Dept. Biology, Queens Coll., Flushing, New York 11367. (Present address: Archbold Biological Station, Route 2, Box 180, Lake Placid, Florida 33852.) Accepted 1 Nov. 1982.
Examining nesting cavities with an optical fiberscope.—Many birds nest in cavities. Tools such as pole-mounted mirrors and lenses mounted on long sticks (Demong and Emlen, Wilson Bull. 87:550–551, 1975) have aided previous observations of nesting cavities, but these methods are suitable only when the cavity entrance has no more than one bend, or when the investigator's arm can reach a point where there is a straight passage to the nest. Using flexible fiber optic devices avoids these restrictions, and allows a clear view of the interior of deep cavities with irregular entrances.

The Olympus GIF Type D optical fiberscope consists of a 1 m flexible cable, 1.3 cm in diameter, with lenses at both ends. An image of the scene before the objective is internally reflected to the ocular by means of coherently arranged flexible glass fibers within the cable. The angle of acceptance at the objective tip is 75°, and the tip can be remotely articulated in two planes. Maximum depth of field is 2 cm to infinity, with resolution better than 1 mm at close range. The minimum bend radius of the image cable is 7.5 cm. The fiberscope's objective can be protected from abrasion by a lens hood made from a plastic bottle. Examination of dark cavities requires illumination; I provided this with a flashlight bulb mounted in the lens hood, but a light source beamed through the fiberscope's internal light guides would serve the same purpose.

I successfully used the fiberscope in searches for Black Guillemot (Cepphus grylle) and Atlantic Puffin (Fratercula arctica) nests in complex boulder habitat. Census work, involving the location of nest cavities and/or the determination of nest occupancy rates, is an important potential use for optical fiberscopes. The other major potential is in breeding studies, where the investigator can remotely monitor the progress of otherwise unobservable nests. These applications are appropriate for nest cavities in soil and trees as well as those among rocks.

Fiberscopes are expensive. New medical instruments cost upwards of $8000, and industrial ones are about half this. But medical devices depreciate rapidly, and my fiberscope was obtained from a local hospital for 15% of its new value. Thus, the used medical equipment market may provide ornithologists with a source for this useful device.

Acknowledgments.—I thank A. Macfarlane, W. E. Cairns, and I. L. Jones for field assistance, and M. B. Fenton for reviewing the manuscript. The study was supported by the Canadian Dept. Supply and Services and the Canadian Wildlife Service.—D. K. Cairns, Biology Dept., Carleton Univ., Ottawa K1S 5B6, Canada. Accepted 21 Feb. 1983.

Seasonal trends in body condition of juvenile Red-tailed Hawks during autumn migration.—Prior to and during migration, many long-distance migrants accumulate massive lipid reserves and increase in weight. In contrast, partial migrants which migrate shorter distances usually show little premigratory fattening. Although most raptors, including the American Kestrel (Falco sparverius), are partial migrants (Newton, Population Ecology of Raptors, Buteo Books, Vermillion, South Dakota, 1979), Gessaman (Wilson Bull. 91:625–626, 1979) reported the occurrence of autumnal premigratory fattening (albeit with lesser relative amounts) in American Kestrels in Utah. We lack published information for other migrant raptors. Here, we describe seasonal variations in amounts of subcutaneous fat, size, weight, and general body condition of 65 juvenile Red-tailed Hawks (Buteo jamaicensis) captured on migration in the autumn of 1981 at Cedar Grove Ornithological Station, located on the shore of Lake Michigan in central Wisconsin.
We captured migrating Red-tailed Hawks in bow-nets and dhogaza nets as described by Mueller and Berger (Wilson Bull. 79:397–415, 1967). At capture we examined each hawk and assessed the amounts of subcutaneous fat visible through the skin on its flank and the relative size of its pectoral muscles. The amount of subcutaneous fat was ranked on a scale from 0 (none)–6 (the largest amount observed). The relative size of the pectoral muscles was assessed by eye using the cross-sectional contour at mid-sternum and rating the shape on a scale from 0 (slightly concave)–3 (well-rounded convex). We assumed that individuals with little subcutaneous fat and concave pectoral muscles were in poorer general condition, either having failed to obtain adequate food to develop fat and muscles or having lost fat supplies and muscle mass as a result of subsequent food shortage (for an example with quail see: Leopold, Game Management, Charles Scribner's Sons, New York, New York, 1933). The scales used here are subjective, but we think they describe adequately the range of variation in the sample. At the end of each trapping day the birds were weighed to the nearest 0.5 g on a triple-beam balance. Wing chord measurements (Mueller et al., Am. Birds 33:236–240, 1979) were also taken at this time.

Juvenile birds tended to migrate earlier than adults but continued to be trapped throughout the migration season (Fig. 1). Although female Red-tailed Hawks average larger in body size than males, there is broad overlap in the size of the sexes in all Red-tailed Hawk populations north of Cedar Grove’s latitude (43°33’N) (Friedmann, U.S. Natl. Mus. Bull. 50, Pt. II, 1950). On the basis of 29 individuals that could be sexed because their wing chords were above or below the zone of overlap (Fig. 2a), we found no difference in the sex ratios of birds between

![Seasonal variation in the proportion of juvenile and adult Red-tailed Hawks trapped during autumn migration.](image)
Fig. 2. Variation in wing chord length (a), subcutaneous fat (b), and pectoral muscle size (c), of juvenile Red-tailed Hawks during autumn migration. See text for explanation of the scales. Because they were tightly clustered, some points may represent more than one datum as indicated by adjacent numerals.

We found larger amounts of subcutaneous fat on hawks trapped later in the migration period. The first half (7 ♀♂: 9 ♀♀) and second half (4 ♂♂: 9 ♀♀) of the migration period ($\chi^2 = 0.513$, df = 1, $P = 0.471$). Thus, the evidence suggests that males and females apparently migrate at the same time.
season (Fig. 2b. Spearman’s r = 0.710, P < 0.01, N = 65). Similarly, there was an increase in pectoral muscle size as the autumn migration progressed (Fig. 2c. Spearman’s r = 0.758, P < 0.01, N = 65). A significant positive correlation existed between the amount of subcutaneous fat and the size of the pectoral muscles (Spearman’s r = 0.645, P < 0.01, N = 65).

Thus, there is a tendency for the largest amounts of fat to be found on birds with large pectoral muscles.

We found no significant seasonal trend in body weights during the migration period (Pearson’s r = 0.095, P > 0.25, N = 65), and there was no relationship between body weight and subcutaneous fat (Spearman’s r = 0.091, P > 0.25, N = 65), or between body weight and the size of the pectoral muscles (Spearman’s r = 0.057, P > 0.25, N = 65). A significant relationship between wing chord and body weight was observed (Pearson’s r = 0.718, P < 0.01, N = 65). Wing chord decreased significantly as the migration progressed (Pearson’s r = -0.318, P < 0.01, N = 65) (Fig. 2a). Thus, there is a tendency for juvenile Red-tailed Hawks with the longest wing chords to migrate past Cedar Grove earliest in the season. Analyses of similar wing chord and body weight data from autumns of 1975 through 1980 at Cedar Grove showed seasonal trends each year that paralleled the trends in 1981.

We found wing chord length to be corelated inversely with both the amount of flank fat and size of the pectoral muscles (Spearman’s r = -0.293, P < 0.05, N = 65 and Spearman’s r = -0.371, P < 0.01, N = 65, respectively). Thus, the larger birds tended to have less fat and less developed pectoral muscles than smaller individuals.

In summary, observations of 65 juvenile Red-tailed Hawks revealed that those trapped later in autumn migration were increasingly fat, well muscled, and smaller in body size. Thus, many of the largest birds appeared to be in the poorest condition.


Juvenile Red-tailed Hawks trapped at Cedar Grove tended to be largest earlier in the season. In view of the geographic variation in departure dates, our data would be consistent with a geographic trend in body size of Red-tailed Hawks that follows Bergmann’s Rule.

Red-tailed Hawks breed later in the year at higher latitudes (Bent 1937, Orians 1955). For example, in central Alberta (54°23’N), the normal fledging date is mid-July (Luttich et al., Auk 88:75–87, 1971), whereas in southern Wisconsin (43°11’N), near the northern limit of the range in which Red-tailed Hawks are permanent residents, the normal fledging date is early June (Petersen, Wisc. Dept. Nat. Resour. Tech. Bull. 111, 1979).

In view of their later fledging dates and earlier migration, juveniles in northern populations have a shorter time than juveniles farther south to develop their muscles and accumulate fat before migrating. This may account for the hawks that migrate past Cedar Grove earliest being in poorest condition in terms of muscle size and fat reserves. Furthermore, the earliest migrants also may have traveled the longest distance before reaching Cedar Grove and may have depleted their fat reserves while migrating.

ORNITHOLOGICAL LITERATURE

The Emergence of Ornithology as a Scientific Discipline: 1760–1850. By Paul Lawrence Farber. D. Reidel Publ. Co., Dordrecht, Holland; Boston, Massachusetts; and London, England, 1982:191 pp., 4 black-and-white plates. $39.50.—For some years Dr. Paul Lawrence Farber has been interested in the transformation of the earlier undisciplined study of “natural history” into a set of separate scientific specialities during the late eighteenth and early nineteenth centuries. This was a time of profound change in western Europe brought about by the French revolution of 1789 and the later, less abrupt but equally pervasive British industrial revolution, which made so many changes in all aspects of agricultural, commercial, and social conditions in western Europe. In this book Farber presents a case study of the emergence of one of these disciplines—ornithology—chosen because it was among the first and most important areas of natural history to emerge as a serious and well-organized subject. The year 1760, at which this study opens, saw the publication of Mathurin Jacques Brisson’s massive six-volume compendium on all that was then known about birds, “Ornithologie, ou Methode contenant la division des oiseaux en ordres, sections, genres, especes et leurs varietes.” Brisson felt that all the earlier writings on birds were either too inaccurate, or too limited in scope, and generally out of date in their factual presentations, and that the time had come for a new and more comprehensive and reliable compilation. His approach to ornithology was from the perspective of a museum curator, a collection catalogue, much expanded and completed to be sure, but still a rather prosaic description of the external appearance of each of the hundreds of species treated, with emphasis on previously unknown “new” species, and with a new and greatly broadened classification. Brisson’s effort was soon eclipsed by a much larger work by Georges Louis Leclerc, comte de Buffon, whose “Histoire Naturelle . . . avec la description du Cabinet du Roi,” beginning in 1749 and closing in 1804, had a total of 44 volumes. Buffon’s approach to natural history was much broader (not limited just to birds), and included all available information on the habits, geographic ranges, etc., of each species treated, as well as descriptions of their plumage and general appearance. It exerted a wider influence on the intellectual classes of the time than did Brisson’s less readable, less “literary” tomes. Furthermore, it caused many of his well-placed and influential readers to encourage societies and even governments to support and to send out numerous exploring and collecting expeditions to little known regions. These eventually expanded the collections of specimens and of pertinent observations about the fauna of the world. The appearance of Brisson’s and Buffon’s works was fortunately timed as natural history became quite fashionable at that time, and the knowledge of the birds of the world grew very rapidly as a result. Farber gives many details of this dramatic increase in ornithological knowledge. He documents the growth of research collections, both in size and number, and the multiplication of scholarly books and journals. With these great additions there resulted first a new and improved classification, and then a diverse series of studies of the habits and distribution of birds. These developments gave ornithology a scientific and well-organized status as a serious discipline. As an historian of science and of society, Farber examines this one science in terms of its institutional developments, its links with colonization in a period of much “empire building,” and its place with other intellectual interests in a rapidly changing society. It is a book designed more for the historians of science, as a part of culture, than for ornithologists alone.—HERBERT FRIEDMANN.
THE THICK-BILLED MURRES OF PRINCE LEOPOLD ISLAND. By Anthony J. Gaston and David N. Nettleship. Canadian Wildlife Service Monograph Series, No. 6, Ottawa, 1981: 349 pp., 19 color plates, 127 numbered text figs., 87 tables, 28 appendices. $32.00 in Canada, $37.50 in other countries (can be obtained from Printing and Publishing, Supply and Services Canada, Ottawa, Ontario K1A 0S9, Canada. Catalogue No. CW 65-7(6E).—This is an essential book for all those concerned with the ecology of seabirds. The wealth of material it condenses is remarkable and, in addition, the monograph also deals with broad considerations. As stated in the title, this is an in-depth study of a single species at a remote Canadian high-arctic location. The biological and physical environments are described in Chapter I while attendance and behavior at the colony, timing and success of reproduction, development of young, adult weight, food, and feeding areas occupy the succeeding chapters. Each chapter ends with a concise and factual summary. The book ends in a 24-page general discussion (conclusions and general considerations; Chapter VI). The empirical approach employed in the study generated truly impressive quantities of immensely detailed information that have been processed and analyzed in a thorough manner. Despite the density of the material presented, the text is easy reading and abundantly cross-referenced to increase usefulness.

Although being very favorably impressed by this book, I nevertheless have some reservations concerning it. I have the impression that the stated objective “to gather as much information as possible on the reproductive biology and ecological requirements” (p. 21) of the Thick-billed Murre (Uria lomvia) was so broad as to really stifle the perspective of the study. Had more specific questions been asked at the outset of the program, it would have readily become evident that many of the problems could not profitably be studied at Prince Leopold, in view of the very demanding field conditions imposed by the peculiar physical features of the island. The central questions of colony structure, site tenacity, success and failure of known individuals in successive years, sexual differences or similarities in attendance or in sharing the parental duties are all impossible to tackle without marked individuals, but the authors relied on only a handful of such birds. Not surprisingly, the interpretation of the scanty data on these themes lacks the vigor one might have expected in a monograph of this importance.

Some of the information is presented in such detailed fashion as to be of questionable use; this includes numerous “typical” excerpts from note-books. For instance, Figs. 37 and 38 show landing spots used by prospecting birds in one of the study plots in July, 1977. The 28 appendices (64 pages!) contain most of the raw figures upon which the study is based, including weather data, daily counts in various plots, growth data of individual chicks, etc. Undoubtedly, a safe repository must exist in the Canadian government where such information could have simply been stored for future reference.

Finally, the most serious criticism I have about this book concerns Chapter VI. The questions of broad feeding relations among seabird communities of the Arctic, the causes of coloniality, and the factors controlling population size are clearly matters of deep and exciting intellectual interest and importance. However, the authors themselves confess that the key to understanding these fundamental relations lies in the distribution and abundance of the marine food upon which these birds depend. Since this factor was not investigated, the entire chapter becomes rather disconnected from the major themes of the study, although it is lucidly written.

The book is splendidly produced with color photographs for the front and back covers, along with the 19 color plates. It is attractively laid out on heavy glossy paper and, considering the price, is a real bargain as books go these days. The discussion of many challenging aspects of seabird ecology which the monograph presents (including Chapter VI, despite my above comments) is well worth the money. The development of field study techniques with careful assessment of their limitations will also remain a useful, in fact essential, contribution
for years to come. Such techniques have since been applied to other colonies of the Canadian Arctic and numerous results from these comparative investigations have now appeared in print or are forthcoming.

Gaston and Nettleship have made with this book a monumental contribution to the literature on seabirds and I feel a deep sense of respect and admiration at such a massive undertaking and at such a detailed and thorough outcome. It will remain a classic contribution despite the limitations which I have pointed out.—Jean Bédard.

The Birds of Borneo. By Bertram E. Smythies. Illustrated by Commander A. M. Hughes. Third edition revised by the Earl of Cranbrook. The Sabah Society with the Malayan Nature Society. 1981:xiii + 473 pp., 46 color plates, 4 black-and-white plates, 2 line drawings, 1 map. Order from the Sabah Society, P.O. Box 547, Kota Kinabalu, Sabah, East Malaysia. MR$55, plus MR$6. postage and handling.—For years Smythies' classic has been out of print and unavailable to all except those who could afford the time and expense to track down a copy. The demand from an increasing number of bird-watchers in Borneo and the desire on the part of conservationists to spread information on wildlife in Southeast Asia prompted Malaysia's major natural history groups, the Sabah Society and the Malayan Nature Society, to organize the publication of a third edition. Their efforts have paid off well. The new book fills a tremendous gap and ends years of frustration for bird enthusiasts and scientists alike.

Five thousand copies of this revised edition have been printed under the supervision of the Earl of Cranbrook, who as a contributor to the original work (a chapter on cave swiftlets [Colidocalia]) and a long-time Bornean mammalologist and ornithologist was a logical choice as editor. For the Malaysian societies, which have limited memberships, the cost of publication of this number of books was no small problem. The success of their venture has stemmed largely from the support given by the Sabah Foundation, a quasi-governmental organization which uses money earned from an extensive logging concession to fund educational and other projects in Sabah. The Foundation agreed to buy 2500 copies at list price for use in the schools and libraries of Sabah, thereby helping to cover printing costs while contributing to a major goal of the republication—the increase of interest and awareness of local people in wildlife. The new edition must be viewed in light of this need for a bird-watching and educational guide as well as the desire of its sponsors to produce the book quickly and cheaply. Otherwise, readers who are familiar with the "book collector" quality of the earlier editions and those who expect a sophisticated, modern handbook will be somewhat disappointed.

The original book has been changed considerably by the deletion of the introductory chapters and photographs. As Cranbrook points out in the introduction to the new edition, this is largely an economy measure. Much of the supplementary information was either superfluous to a bird guide (certainly the photographs and J. D. Freeman's anthropological chapters) or outdated (Cranbrook's own chapter). Such cuts really only detract from the historical value of the book, but this is still a sad concession to modern realities.

In its new format, the third edition consists almost entirely of species accounts. Having been reproduced by a money-saving facsimile process, these appear essentially as they did in the 1968 edition. New information on selected species has been added in smaller type by Cranbrook at the end of their accounts. This method has the advantage of retaining some of the flavor of Smythies' original work, but unfortunately it also retains some of the major short-comings, not the least of which are the bird descriptions. A classic, but by no means unique, example of one of these poorer descriptions is that of the Pied Imperial Pigeon.
(Dacula bicolor): "Unmistakable. Iris black, bill and feet brown." Smythies' keys to bird identification are another problem. Several are incomplete or require greater knowledge of the families than much of the public has. Others are simply irritating. For example, in the description of the Pygmy Blue Flycatcher (Usceicapella hodgsoni), the reader is sent to the key for details only to find that this species is not included there. To birders used to modern standards in bird books, this lack in information can be infuriating. Surely a more thorough revision would have addressed these weaknesses.

However, the supplementary information provided by Cranbrook helps in bringing up to date the knowledge of other aspects of Bornean bird natural history. He has drawn heavily from published and personal notes of bird watchers in Brunei and Sabah, thus strengthening the shorebird and migrant accounts and increasing the geographic scope of the book. (Previously, The Birds of Borneo dealt almost exclusively with the birds of Sarawak and Mt. Kinabalu, with only spotty references to other localities.) Data have been included from a few recent scientific expeditions as well, such as the Royal Geographical Society expedition to Mt. Mulu in Sarawak. Records gathered with the use of mist-nets and tape recorders on these expeditions have helped to correct misconceptions about the status of several birds. The endemic Bornean Wren Babbler (Ptilocichla leucogrammica) and the Chestnut-capped Thrush (Zoothera interpres) are examples of species formerly thought to be rare, but now known only to be secretive.

Unfortunately, the amount of information accumulated over the past 10-20 years and available to Cranbrook is really quite scanty, in spite of enormous improvements in transportation and habitat accessibility brought about by the logging boom. For an avifauna so circumscribed as Borneo's, it is surprising that so little has been learned. Breeding and nesting are particularly poorly understood. The new edition of The Birds of Borneo is still replete with, "Nest and Eggs. Nothing recorded from Borneo." or simply, "Unknown," even for common species. Some gaps are now being filled in Sabah, where the most active research is taking place; but Kalimantan, the Indonesian part and by far the largest section of Borneo, remains unstudied. Almost no new information has come from there since colonial days, and this dearth of knowledge is reflected in the third edition. Without extensive field work and museum and library digging (in Dutch), nothing more can be said about its birds.

These problems aside, the new The Birds of Borneo fulfills its chief function as a reference on Bornean birds. Cranbrook has enhanced its effectiveness by bringing Smythies' old common names into accord with the simpler, modern forms proposed in King, Woodcock, and Dickinson, A Field Guide to the Birds of South-East Asia, a widely used book, although not technically covering Borneo. Gone are the likes of the Brown Quaker Babbler and the Crestless White-throated Bulbul, now replaced with the Brown Fulvetta and Yellow-bellied Bulbul. In addition, Commander Hughes' excellent plates, which were a milestone 20 years ago for their quality and completeness, have been included in their entirety and are fairly well reproduced. Combined, these two books make possible the identification of essentially all the Bornean birds. Without a copy of Smythies, this just is not possible.—FREDERICK H. SHELDON.

A DISTRIBUTIONAL CHECKLIST OF THE BIRDS OF MICHIGAN. By Robert B. Payne. Miscellaneous Publications, Museum of Zoology, University of Michigan. No. 154, 1983:71 pp., 1 map. $9.50.—This work summarizes the occurrence, breeding status, migration, and distribution of the birds of Michigan. Of 370 species known from the state, 232 have bred under natural conditions, one (Passenger Pigeon) is extinct, some have not been seen recently, and others are recent additions to the state list. The list includes 26 "hypotheticals" whose
 occurrence is not considered rigorously documented by specimens or photographs. There are also a few “rejected” species of doubtful occurrence. This compilation of records by many observers and museum records will aid field workers to identify birds, and will serve as a basis for studying long-term changes in the avifauna. It includes a map of the counties in the state and an index to scientific and common names.—R.J.R.

**British Birds.** By Ian Prestt. B. T. Batsford Ltd., London and North Pomfret, Vermont. 1982:224 pp., 69 line drawings by Rob Hume. $17.95.—This book was written by the Director of the Royal Society for the Protection of Birds to promote the widest possible interest in British wild birds. Prestt seeks to capture people’s normal curiosity about birds by offering more information about each species than a field guide does while relating them in a simple way to one another and to their environment.

The text is organized by five major habitat groups and covers most regularly occurring British species (slightly over 200) at a level reminiscent of that found in Richard H. Pough’s *Audubon Bird Guides*. The author weaves an impressive amount of information about avian biology and ecological principles around a solid base of behavioral and identification data pertaining to most of the species he treats. Thus, under “Woodland” we learn for the Lesser Spotted Woodpecker (*Dendrocopos minor*) that it “... is finch-size, secretive and spends much time feeding near the tops of trees... Its light weight and small size enable it to cling to the smaller, higher branches on which it will search methodically for insects, fluttering to a neighboring branch as it finishes the one it is on. It is frequently in the same woods as the Great Spotted Woodpecker (*Dendrocopos major*), but the separation in feeding sites in particular excludes competition...” The book’s organization by habitat, which might be disconcerting in a field guide, is effective in conveying the ecological relationships among the species covered.

If I was disappointed at all, it was in the fact that some species, mostly ones rare in Britain, were discussed only superficially. The rather succinct and unillustrated field descriptions often seemed almost superfluous in the face of the author’s recommendation that readers supplement the book with a popular field guide. In the main, however, Prestt achieved his goals well. His unimposing style would appeal even to an older child. Rob Hume’s delightful line drawings enhance the book’s charm tremendously.

**British Birds** is pleasant, easy reading, and an important complement to all-too-pithy modern field guides. An American unfamiliar with European avifauna who might be planning a birding jaunt to Britain would find it particularly helpful for showing in some detail the favored habitat and normal behavior of most species to be expected. It also would be an excellent model for anyone contemplating writing a regional book intended to expand the public’s awareness of birds and how they fit into the environment.—P. William Smith.

**Falkland Islands Birds.** By Robin W. Woods, photographs by Cindy Buxton, Annie Price, and Robin W. Woods. An Anglia ‘Survival’ Book, Anthony Nelson. P.O. Box 9, Oswestry, Shropshire SY11 1BY, England. 1982:79 numbered pp., 32 unnumbered pages with 58 color and 5 black and white photographs, 1 text figure, 1 table, map end papers, index. £8.50 (approximately US$12.75).—This attractive, sturdy bound, pocket-sized (5½” x 8”) book presents non-technical species accounts for 67 birds common in the Falkland Islands and photographs, most of them outstandingly beautiful, of 53 species. There is a
useful checklist of the 152 species recorded for the Falklands, the status of each indicated by code letters.

A brief introduction describes the geography, climate, and vegetation of the islands and discusses origins and elements of the avifauna and its distribution. This is followed by a “habitat table” for the 67 common species. While not a comprehensive field guide, this work is a useful introduction to the bird life of the Falkland Islands and serves as an excellent popular guide to the common species there. A section on “Further reading” will help the enthusiast find more detailed information.—PHILIP S. HUMPHREY.

GOLDEN EAGLE YEARS. By Mike Tomkies. William Heinemann, London. Dist. by David & Charles, Inc., North Pomfret, Vermont. 1982:202 pp., 22 color plates, 42 black and white photos, appendices. $24.95.—The book is basically a journal written during the time Mr. Tomkies was living in the wilderness of the western Scottish highlands making a photographic record of the breeding cycle of eagles with observations and comments on their annual cycle. While this book has limited appeal to me—it is not done with any scientific rigor—it will obviously excite some. The writing style is good, his syntax interesting, but I got bored with the chronicled detail of his sitting in blinds, stumbling down brushy mountain slopes, and notations of minor and sundry sightings of eagles flying here and there. In all, there are 17 chapters, the first four of which describe the author’s various wanderings around the hills looking for nests and breeding pairs. Chapter titles indicate fairly well the content of the chapter, such as, chapter 10—“Eaglets Growing Up—Their First Flight,” and chapter 11—“A New Mate For Atlanta.”

The underlying theme of the book seems to be that since the Golden Eagle (Aquila chrysaetos) is a scarce bird in parts of Europe and Britain itself (other than Scotland), the author was breaking new ground. It was often hard for me to focus on his perspective and treat it objectively. For example, in my own state of Utah there is something on the order of 2500 to 3000 pairs of Golden Eagles. That number is similar to populations in the entire area of most of western Europe as a quick review of Cramp and Simmons (The Birds of the Western Palearctic, Vol. II, Oxford Univ. Press, 1980) will show. Thus Britain, with 200–300 pairs, may have as much as 10–15% of the European population (the author says 25%). And, I suppose that if I lived in a country like West Germany with 15–17 pairs, or Poland with 8–10 pairs, then I would find the Golden Eagle an intriguing and little-known species or at least rare enough that such a book would excite me.

The manner of presenting the data on all the eyries he found bothered me a bit. The eyries were simply listed and mentioned by giving them by number, e.g., “a new eyrie located between 12 and 4/5.” This has little meaning for it is impossible to determine how far apart the eyries were, what the terrain was like in the area of the eyrie, etc. A good map showing the distribution of eyries relative to one another (showing which ones were alternate for a pair) would have been of scientific interest. Aside from the lack of rigorous data presentation, several noteworthy observations were made by Tomkies during his 7-year study. For example, in the autumn he saw a yearling eagle attack and grab onto a deer calf that he estimated to weigh 50 lbs. The eagle was unsuccessful in subduing it. He also noted that adult eagles flew back to their nests well after dark, as late as 11:15 pm, often with food.

The photos are of variable quality and some could have been entirely omitted. Many are blurred. On the other hand, several of the color photos are particularly good. Some clearly showed the generally paler color of the European race, as opposed to the North American one, such as I had never before seen it. I especially liked one photo of an adult with a sprig of greenery in its bill (p. 139), one of the adult landing at the nest with wings in a half opened
position (p. 174), and one of a young eagle soaring over the beautiful heather-covered Scottish landscape. All in all, this book may appeal to a certain type of ornithologist or nature lover, but I found little meaningful biology in it. This is unfortunate because, after all the time and energy the author put into his study, he could have, with a certain precision of data presentation or different organization, made a much more interesting contribution.—Clayton M. White.

Morphological Similarities Between the Menurae and the Rhinocryptidae. Relict Passerine Birds of the Southern Hemisphere. By Alan Feduccia and Storrs L. Olson. Smithsonian Contrib. Zool. No. 366. Smithsonian Institution Press, Washington, D.C., 1982:iii + 22 pp., 17 black-and-white figs., 1 table. Price not given.—Feduccia and Olson studied the osteology of several passerine groups. They found that in the rhinocryptid genus Melanopareia the stapes (middle ear ossicle) is of the primitive type, which excludes this form from the main suboscine assemblage defined by the derived stapes previously described by Feduccia. However, Melanopareia does possess the derived tracheophone syrinx, which places it in the Furnarioidea, a suboscine subgroup. These characters are therefore in conflict. They also found that the osteology of the Menurae is unlike that of the Ptilonorhynchidae or Paradisaeidae, in contrast to recent suggestions. Additionally they report many similarities in the osteology of the Menurae and the Rhinocryptidae. Based on these studies Feduccia and Olson conclude that “the Menurae and the Rhinocryptidae are among the most primitive of the Passeriformes and are representative of the ancestral stock that gave rise to the remainder of the passerines.” Being reluctant to separate the concepts of similarity and genealogy, they do not settle on a single criterion of relationship through which specific phylogenetic hypotheses might be proposed. Nevertheless, they do suggest a number of biogeographic and adaptational hypotheses about the origin of the Passeriformes and their major subgroups.—Robert J. Raikow.


World Inventory of Avian Spirit Specimens, 1982. By D. Scott Wood, Richard L. Zusi, and Marion Anne Jenkinson. American Ornithologists' Union and Oklahoma Biological Survey, Norman, Oklahoma, 1982:181 pp. $25.00.—Computer technology and much hard work by the authors has made a major new resource available to the ornithological research community. These inventories will greatly facilitate the management and growth of museum collections of specimens, as well as the planning of collection-based projects. It will no longer be necessary for investigators to write to curators in many different museums to find out what materials are available, often overlooking collections in the process. Instead one can turn to these bound computer printouts and immediately learn how many specimens of what species are held in virtually all major collections.

The two inventories are organized similarly. After a brief introduction and acknowledgments there is a list of the museums inventoried and summaries of the numbers of specimens that they possess. This is followed by a list of the addresses and curators of the museums: an index to the orders, families, and subfamilies of birds; and an index to the genera.
including synonyms. The major part of each work is the inventory itself, in the form of a long table. To use it you merely find the desired species (aided by the indexes if necessary) and read across to see how many specimens are held by each of the museums listed. In the inventory of spirit specimens all 41 museums are included in one table. The skeletal inventory includes the 45 largest collections in the main table, plus an appendix with 44 smaller collections.

The history of the project and an analysis of the data were previously discussed by the authors (Auk 99:740–757, 1982). Every museum with anatomical collections, and every researcher using such collections will need a copy of one or both of these valuable compilations. They may be ordered from the Oklahoma Biological Survey, Sutton Hall, University of Oklahoma, Norman, OK 73019, U.S.A. The price includes surface postage; airmail is additional. Wood, Zusi, and Jenkinson deserve the gratitude of avian anatomists and systematists for producing these works, which will rapidly become indispensable to the efficient conduct of research.—ROBERT J. RAIKOW.

REVIEW UPDATE

In his complimentary review (Wilson Bull. 94:604, 1982) of "Voices of New World Nightbirds," ARA-6 (1980), a record album that I produced and narrated, R. M. Mengel briefly discusses the two examples of song of the Little Nightjar (Caprimulgus parvulus) on the disc (see his next to last paragraph) and states that the first of these is of a bird of a population now regarded as a distinct species, C. anthonyi (Schwartz, Condor 70:223–227, 1968). Dr. Mengel's statement is incorrect. C. anthonyi was, as Schwartz (1968) says, considered a race of C. parvulus by Peters (Check-list of the birds of the world, Vol. 4, 1940). C. anthonyi is a bird of western Ecuador, west of the Andes, and to my knowledge there are no recordings of its voice. Schwartz separated it in his article solely upon morphological characteristics with some discussion of possible ecological difference as well. On the record album, side 2, cut 73, example 1 is of a bird recorded by Ben B. Coffey, Jr., near Yarinacocha, Peru, on the eastern side of the Andes, in the upper Amazonian drainage. The area is within the range of C. p. parvulus (Peters 1940:202). Example 2 of cut 73 was of a Little Nightjar (race C. p. heterurus) recorded 1 mi S Petare, Venezuela, by Paul Schwartz. The Peruvian and Venezuelan birds have strikingly different songs, and so the point is that even within the currently recognized range of the Little Nightjar, there are at least two vocally different forms and possibly, therefore, more than one species "hiding" under the binomial C. parvulus. However, the matter certainly needs further investigation, as the songs of the two birds are certainly no more different than those of eastern and western Rufous-sided Towhees (Pipilo erythrophthalmus) in North America. Considering the greater stereotypy that nightbirds show in their species-specific territorial songs, it is my judgement that differences in vocalizations as great as those shown between these Peruvian and Venezuelan Little Nightjars is more significant with respect to possible unrecognized species than are differences in primary song of diurnal birds such as towhees.—JOHN WILLIAM HARDY, Curator in Ornithology and Bioacoustics, The Florida State Museum, Univ. Florida, Gainesville, Florida 32611. Received 9 June 1983.
ORNITHOLOGICAL NEWS

REQUEST FOR ASSISTANCE

Adult and nestling Turkey Vultures in Wisconsin are being marked with green patagial wing tags during 1983 and 1984, as part of a study of nest and roost fidelity, feeding ranges, and migration. Tags are encoded with a small "U" and large white numerals, 1-99. If marked vultures are sighted, please report date, location, tag number, whether tag is on right or left wing, and other pertinent observations to the Bird Banding Laboratory, U.S. Fish and Wildlife Service, Laurel, Maryland 20811; and to Madison Audubon Society, Rt. 1 Box 128A, Arlington, Wisconsin 53911.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following opinions were published by the ICZN in Bull. Zool. Nomenclature, Vol. 40, Pt. 2, 15 July 1983.—1249 (p. 83) Toxostoma crissale ruled to be the correct original spelling of the name first published as Toxostoma dorsalis Baird, 1858 (Aves); 1252 (p. 90) Sterna cerulea Bennett, 1840 (Aves); conserved.

Erratum.—Vol. 95, No. 1, “Cowbird parasitism of Dickcissels in different habitats and at different nest densities” by John L. Zimmerman: p. 9, second line under the heading Habitat Differences, 235 prairie nests should read 125 prairie nests.
The Wilson Bulletin

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Suggestions to Authors

See Wilson Bulletin, 91:306, 1979 for more detailed “Suggestions to Authors.” Manuscripts intended for publication in The Wilson Bulletin should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Checklist (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in “General Notes” should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the “CBE Style Manual” (1972). AIBS). Photographs for illustrations should have good contrast and be on glass paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 x 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.
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If 1^
Adult female Bluish-slate Antshrike. Gouache painting by F.P. Bennett, Jr.
FORAGING BEHAVIOR, ECO-MORPHOLOGY, AND SYSTEMATICS OF SOME ANTSHRIKES
(FORMICARIIDAE: THAMNOMANES)

THOMAS S. SCHULENBERG

The external morphology of a bird is a reflection of two factors: phylogeny and adaptations to the environment. Traditionally birds have been classified by systematists on the basis of similarities in morphology, especially at lower taxonomic ranks. Ecologists frequently study the same morphological characters used by systematists (e.g., Hespenheide 1973, Karr and James 1975, Ricklefs and Cox 1977). When taxa are arranged on the basis of characters influenced by ecological adaptations, are the resulting classifications reflections of ecological similarity, phylogeny, or both?

The present study is an eco-morphological and systematic study of Thamnomanes, a genus of six species of tropical South American antshrikes (Formicariidae). The majority of the species of antshrikes (Thamnophilus, Dysithamnus, and related genera) are generalized perch-gleaning insectivores. Several species of Thamnomanes, however, have recently (Oniki and Willis 1972, Pearson 1975, Munn and Terborgh 1979, Wiley 1980) been recognized to have a specialized “fly-catching” foraging behavior, characterized by a distinctive upright posture (Frontispiece), a “sit-and-wait” foraging strategy, and long prey-capture sallies. These features of Thamnomanes foraging behavior are all more typical of families other than the Formicariidae (e.g., Tyrannidae, Bucconidae, Galbulidae). The foraging behavior of Thamnomanes appears to represent an evolutionary “experiment” in “fly-catching” behavior unique within the Formicariidae. The aim of this study is threefold: to obtain quantified information on the foraging behavior of Thamnomanes antshrikes; to determine what, if any, morphological adaptations accompany this divergent foraging behavior; and to use this information to reconsider the systematics of the genus.
STUDY SITES AND METHODS

Field observations of Thamnomanes were made at two study sites. Two species, Bluish-slate Antshrike (Thamnomanes schistogynus) [Frontispiece] and Dusky-throated Antshrike (T. ardesiacus), occur at the first study site, the Explorer’s Inn (12°40’S, 69°15’W), elev. 260 m, Dept. Madre de Dios, Peru; only T. schistogynus occurs at the second site, on the Río Beni, about 20 km by river north of Puerto Linares (ca. 15°24’S, 67°33’W), elev. 600 m. Dept. La Paz, Bolivia. I was at the Explorer’s Inn from 31 October–11 December 1979 and at the Río Beni site from 5 June–8 July 1981. Both study sites are tropical lowland forest (Subtropical Moist Forest Life Zone: Unzueta 1975; OERN 1976). The forest at these sites has never been cleared, although both localities have experienced minor human disturbance. The canopy was tall at both localities; 30–40 m at the Explorer’s Inn, and 30 m at the Río Beni. The forest was structurally similar at the two sites, although the Río Beni site had more treefalls, which are usually sites of dense vine tangles. These tangles are favored foraging sites for many perch-gleaning antbirds, including some with which Thamnomanes spp. regularly forage. The Río Beni site is also more hilly than the Explorer’s Inn site, which has very little relief.

Data were gathered by locating a flock containing foraging Thamnomanes and following the flock as long as possible (on occasion up to 2 h). For comparison to Thamnomanes, I quantified the foraging behavior of two more typical antshrikes, Black-capped Antshrike (Thamnophilus schistaceus) and Plain Antvireo (Dysithamnus mentalis), at the Río Beni study site. I recorded the type of foraging motion, distance of all prey-capture flights, foraging substrate, and height above the ground for each foraging motion. Data were recorded continuously about a bird until I lost contact with it.

Morphological data were taken from museum study skins. The length of the wing (chord), tarsus, and culmen (from base), depth of the hill at the nostril, and the width of the hill at the gape and anterior edge of the nostril were measured with dial calipers to the nearest 0.1 mm. Body weight was recorded from the specimen label.

Most analyses were performed using a minimum of five specimens per species. Data were analyzed using two different statistical procedures, a Mann-Whitney U-test (two-tailed) on ratios of characters and an analysis of covariance (ANCOVA) on linear regressions between characters. The relative length of the wing and tarsus were assessed by comparing these parameters to the cube root of body weight (Amadon 1943). Adequate sample sizes for weight data were available for only three species of Thamnomanes (Cinereous Antshrike T. caesium, T. schistogynus, and T. ardesiacus), and 10 species of Thamnophilus and D. mentalis. The relative shape of the bill was assessed by comparing bill width to culmen length; because this analysis was not dependent upon weight data, more species of Thamnomanes, Thamnophilus, and Dysithamnus could be compared.

Samples from various localities were pooled because geographic variation in size was minor. I followed the taxonomy of Meyer de Schauensee (1970), with one exception. Central and South American populations of Slaty Antshrike (T. punctatus) were treated separately, as there is a significant size difference between the two populations in the specimens examined for this study (8 g difference in population means, with no overlap), and they may not be conspecific (Oniki 1975).

Wing tracings were made from antbirds collected at the Río Beni site. These were made by spreading the open wing flat onto a piece of paper, with the anterior edge in a straight line, and with the remiges evenly spread.

Foraging behavior.—A variety of terms, not always clearly defined, have been used to describe the prey-capture motions used by insectivorous birds. The terminology I use is based on that of Fitzpatrick (1980).

(1) Perch-glean—stationary prey is removed from a substrate while the bird is perched.
Table 1
Prey-capture Motion, Sally Distance, and Prey-capture Substrate of Four Species of Antshrikes

<table>
<thead>
<tr>
<th>Prey-capture motion</th>
<th>D. mentalis N = 60</th>
<th>T. schistaceus N = 19</th>
<th>T. artesiacus N = 38</th>
<th>T. schistogynus N = 84</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sally-glean</td>
<td>15 (25%)</td>
<td>14 (73.7%)</td>
<td>36 (94.7%)</td>
<td>76 (90.4%)</td>
</tr>
<tr>
<td>strike</td>
<td>11 (18.4%)</td>
<td>12 (63.2%)</td>
<td>22 (57.9%)</td>
<td>49 (58.3%)</td>
</tr>
<tr>
<td>hover-glean</td>
<td>4 (6.6%)</td>
<td>2 (10.5%)</td>
<td>14 (36.8%)</td>
<td>27 (32.1%)</td>
</tr>
<tr>
<td>Aerial-hawk</td>
<td>—</td>
<td>—</td>
<td>1 (2.6%)</td>
<td>7 (8.3%)</td>
</tr>
<tr>
<td>Perch-glean</td>
<td>45 (75%)</td>
<td>5 (26.3%)</td>
<td>1 (2.6%)</td>
<td>1 (1.2%)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sally distance (m)</th>
<th>N = 15</th>
<th>N = 14</th>
<th>N = 25</th>
<th>N = 71</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>0.3</td>
<td>0.5</td>
<td>1.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Range</td>
<td>0.2–0.3</td>
<td>0.2–1.0</td>
<td>0.1–4.6</td>
<td>0.1–4.6</td>
</tr>
<tr>
<td>Substrate</td>
<td>N = 58</td>
<td>N = 19</td>
<td>N = 27</td>
<td>N = 74</td>
</tr>
<tr>
<td>Air</td>
<td>—</td>
<td>—</td>
<td>1 (3.7%)</td>
<td>7 (9.4%)</td>
</tr>
<tr>
<td>Leaf</td>
<td>46 (79.4%)</td>
<td>18 (95%)</td>
<td>24 (88.9%)</td>
<td>56 (75.7%)</td>
</tr>
<tr>
<td>top surface</td>
<td>6 (10.3%)</td>
<td>—</td>
<td>3 (11.1%)</td>
<td>10 (13.5%)</td>
</tr>
<tr>
<td>bottom surface</td>
<td>26 (44.8%)</td>
<td>10 (53%)</td>
<td>11 (40.7%)</td>
<td>21 (28.4%)</td>
</tr>
<tr>
<td>surface ?</td>
<td>11 (19.0%)</td>
<td>8 (42%)</td>
<td>10 (37.1%)</td>
<td>24 (32.4%)</td>
</tr>
<tr>
<td>dead leaf</td>
<td>3 (5.2%)</td>
<td>—</td>
<td>—</td>
<td>1 (1.3%)</td>
</tr>
<tr>
<td>Branch</td>
<td>12 (20.6%)</td>
<td>1 (5%)</td>
<td>2 (7.4%)</td>
<td>11 (14.9%)</td>
</tr>
<tr>
<td>&lt;=5 cm</td>
<td>12 (20.6%)</td>
<td>1 (5%)</td>
<td>1 (3.7%)</td>
<td>9 (12.2%)</td>
</tr>
<tr>
<td>&gt;5 cm</td>
<td>—</td>
<td>—</td>
<td>1 (3.7%)</td>
<td>2 (2.7%)</td>
</tr>
</tbody>
</table>

(2) Sally-glean—stationary prey is removed from a substrate by a pursuit flight from a perch. Sally-gleans may be further divided into “hover-gleans” and “strikes.” In a hover-glean, the bird performs a brief hover at the substrate as the prey is captured, whereas in a strike the capture is performed with a flight that carries the bird up to and away from the substrate in a single rapid movement.

(3) Aerial-hawk—flying prey is captured in the air by a pursuit flight from a stationary perch (sometimes referred to as “true flycatching”).

The foraging behavior of most antshrikes (Thamnophilus, Dysithamnus, and allies) is not well known. Antshrikes seem to be primarily generalized foliage-gleaning insectivores. As with other gleaning insectivores, e.g., wood-warblers (Parulini), prey is captured by perch-gleaning or by short sally-gleans (e.g., Oniki 1975, Jones 1977). Due to the paucity of careful field observers in the New World tropics and to the generally secretive nature of these birds, little is known about the relative frequency of perch-gleaning vs sally-gleaning, average sally distance, and substrate utilization.

RESULTS

Quantified data on the foraging behavior of D. mentalis, T. schistaceus, and two species of Thamnomanes are shown in Table 1. Dysithamnus
mentalis is primarily a perch-gleaner, very short sally-gleaning accounting for only a quarter of all observed prey captures. Thamnophilus schistaceus, in contrast, is predominately a sally-gleaner that forages methodically in vine tangles, and often makes short sally-gleans to surrounding vegetation.

Although T. schistaceus is predominantly a sally-gleaner, it does not approach Thamnomanes in the degree of specialization for sally-gleaning. Three parameters of the foraging behavior of Thamnomanes reflect adaptations of this genus to sally-gleaning (Table 1): (1) the almost total absence of perch-gleaning; (2) the addition of aerial-hawking to the foraging repertoire; and (3) the longer sally in Thamnomanes. The sally distance data may be biased towards shorter, easier-to-observe sally-gleans, because the longer the sally, the greater the chance of losing sight of the bird before the moment of prey capture, and of being unable to distinguish a foraging flight from a flight to a new perch.

The foraging behavior of the two Thamnomanes studied may also differ from that of T. schistaceus in two additional parameters, foliage density of the foraging station and length of time spent searching for prey at each foraging station. Thamnomanes typically perch in relatively open sites in the forest understory, unlike Thamnophilus, which typically inhabit rather densely vegetated undergrowth. Fitzpatrick (1981) showed that median search time in tyrannid flycatchers is correlated with foraging strategy: perch-gleaning tyrannids spend less time at each foraging station than do sally-gleaning species. My impression is that a similar pattern could be found in antshrikes: quantification of these parameters is desirable.

Most sally-gleans by Thamnomanes are strikes, which are often explosively rapid. Hover-gleaning is also commonly used. The relative contribution of each prey capture technique to the overall foraging behavior of the two species of Thamnomanes observed is remarkably similar. The major difference between the two is the shorter mean sally distance of T. ardesiacus (1.0 m vs 1.4 m, \( t = 1.94, P < 0.05 \)).

Other authors have also noted similarities in the foraging techniques of syntopic T. ardesiacus and T. caesius (Oniki and Willis 1972, Pearson 1975, Wiley 1980), and T. ardesiacus and T. schistogynus (Munn and Terborgh 1979). It is not clear how syntopic sally-gleaning antshrikes minimize potential interspecific competition. As T. schistogynus and T. ardesiacus differ in their mean sally distance, this may suggest that they are searching for prey at slightly different distances from their perches. Pearson (1977) showed that several species of antwrens (Myrmotherula spp., Warbling Antbird [Hypocnemis contator]) differ in resource utilization patterns in vertical foraging height and foraging substrate. At the Explorer's Inn T. ardesiacus and T. schistogynus use similar substrates, primarily leaf surfaces. There was a difference in perching height (\( t = 7.826, P < 0.001 \))
between *T. ardesiacus* (\(\bar{x} = 2.6 \pm 1.4\) m, range 0.3–10.7 m, N = 221) and *T. schistogynus* (\(\bar{x} = 4.0 \pm 2.4\) m, range 0.3–12.2 m, N = 235). Thamnomanes ardesiacus has previously been noted to forage lower than *T. schistogynus* (Munn and Terborgh 1979) and *T. caesius* (Oniki and Willis 1972). Despite this vertical segregation, however, there is considerable overlap in foraging height between *T. ardesiacus* (\(\bar{x} = 2.9 \pm 1.1\) m) and *T. schistogynus* (\(\bar{x} = 5.1 \pm 2.2\) m) at the Explorer’s Inn.

*Thamnomanes schistogynus* and *T. ardesiacus* regularly forage in mixed-species flocks with each other and with other species of antbirds (Munn and Terborgh 1979; pers. obs.); indeed, I have never seen a *Thamnomanes* that was not associated with other birds. As with other mixed-species assemblages of birds, the benefits to each species from flocking are not clear. Munn and Terborgh (1979) and Wiley (1980) suggested that *Thamnomanes* might derive a feeding advantage by flocking with other birds because other members of a flock might flush insects while foraging that a hawking *Thamnomanes* could capture. Wiley (1980) noted, however, that members of a flock are often spaced so far apart as to make this kind of feeding benefit uncommon. Neither Munn and Terborgh (1979) nor Wiley (1980) reported *Thamnomanes* catching insects flushed by another bird, nor did I observe this. If *Thamnomanes* did not attempt to capture in flight prey items that had been flushed by other birds, but waited until the prey had landed upon a substrate to attempt prey capture, feeding benefits derived from flocking would be difficult to detect by direct field observation. The following observations on the vertical foraging height of *T. schistogynus* suggest indirect evidence of such feeding advantages.

At the Explorer’s Inn site, *T. schistogynus* typically foraged in forest understory. The average perching height of foraging *T. schistogynus* at this locality was 4.0 ± 2.4 m (N = 235), and the average height at which sally-gleans were performed was similar, 5.1 ± 2.2 m (N = 38). Although flocks containing *T. schistogynus* sometimes foraged below mixed-species canopy flocks of insectivorous birds, the antshrikes usually did not change their vertical foraging position in the presence of these flocks, i.e., they did not begin to perch higher to benefit from prey flushed by birds foraging above them.

Perch height was not recorded at the Río Beni study site. At this location, however, *T. schistogynus* regularly left the undergrowth to forage in the lower part of the forest canopy with mixed-species flocks containing such birds as *Tangara* spp., Yellow-crested Tanager (*Tachyphonus rufiventer*), and White-winged Shrike-Tanager (*Lanio versicolor*). This shift in vertical foraging position is reflected in the mean height (9.0 ± 6.1 m, N = 26) at which sally-gleans were performed at the Río Beni, almost twice the mean height at the Explorer’s Inn. The reasons for this vertical
shift are not clear. It is possible that at the Río Beni, *T. schistogynus* actually was joining canopy flocks to capture insects flushed by other flocking species.

**ECO-MORPHOLOGY**

I examined four morphological characters thought to be directly related to prey capture: wing, tarsus, bill, and rictal bristles.

*Wing.*—Most passerine birds, and all formicariids, share a single basic wing design, the elliptical wing. This design provides maneuverability and high lift efficiently at low to moderate speeds (Savile 1957).

Several groups of highly aerial feeders, including some passerines (Hirundinidae, Artamidae), have independently evolved long, narrow, pointed wings. This wing design produces a moderately high aspect ratio (wing span/2/wing area). Fitzpatrick (1978) demonstrated that within the Tyrannidae, relative wing length and aspect ratio varied in accordance with foraging behavior. Relatively longer wings and higher aspect ratios were found in species such as aerial hawkers that made longer pursuit flights for their prey. Consequently, I predicted *Thamnomanes* would have longer wings, with higher aspect ratio, than perch-gleaning antshrikes.

The relative length of the wing (wing length/cube root of body weight) is greater in *Thamnomanes* than in *Thamnophilus* (Fig. 1A; $P < 0.002$, Mann-Whitney $U$-test). Wing lengths of *Thamnophilus* and *Thamnomanes* are also significantly different after the effect of size is reduced ($P < 0.001$, ANCOVA).

To test the hypothesis that the long wings of *Thamnomanes* are correlated with an increase in aspect ratio in sally-gleaning antshrikes, aspect ratios were calculated for 25 species of antbirds (including *T. schistogynus*) from the Río Beni study site (Fig. 2). *Thamnomanes* does not have an appreciably higher aspect ratio than *D. mentalis*, the three species of *Thamnophilus* or most other antbirds whose wings were examined. The highest aspect ratios were found primarily in some antbirds feeding on or near the ground (i.e., Banded Antbird [*Dichrozona cincta*], Scale-backed Antbird [*Hylophylax poecilonota*], Hairy-crested Antbird [*Rhegnatorhinia melanosticta*], and Black-faced Antthrush [*Formicarius analis*]).

The wings of *T. schistogynus*, despite their greater length, have essentially the same shape as the wings of the perch-gleaning *Thamnophilus*

---

**Fig. 1.** Comparative morphology of antshrikes, expressed as ratios of: (A) wing length to cube root of body weight in 10 species of *Thamnophilus* and three species of *Thamnomanes*; (B) tarsus length to cube root of body weight in 10 species of *Thamnophilus* and three species.
A  WING LENGTH/CUBE ROOT of WEIGHT

THAMNOPHILUS

THAMNOMANES

B  TARSUS LENGTH/CUBE ROOT of WEIGHT

THAMNOPHILUS

THAMNOMANES

C  BILL WIDTH/CULMEN LENGTH

THAMNOPHILUS and DYSITHAMNUS

THAMNOMANES

of Thamnomanes; and (C) bill width at the nares to culmen length in 14 species of Thamnophilus, five species of Dysithamnus and five species of Thamnomanes.
and *Dysithamnus*. Wing shape in *Thamnomanes* is probably a compromise between several competing factors. Long wings are favored for sustained flights and for hover-gleaning (Norberg 1979). Wing length is limited however by the somewhat closed vegetation in which *Thamnomanes* forage. Broad, rounded wings are found in many birds that repeatedly make sudden take-offs, as foraging *Thamnomanes* do (Savile 1957). Rounded wings have “slots” at the wing tip, which further increase lift (Savile 1957). Fitzpatrick (1978) found that rounded, slotted wings are typical of many understory sally-gleaning tyrannids.

The relatively greater wing length in *Thamnomanes* is also reflected in relative increase in wing area. Wing area in birds is correlated with weight (Greenewalt 1962). Nonetheless *T. schistogynus* has a relatively large wing area, resulting in low wing-loading (Fig. 3). Lower wing-loading facilitates hovering (Partridge 1976, Norberg 1979), and *T. schistogynus* regularly hover-gleans.

*Tarsus*.—The length of the tarsus in antshrikes may be affected by at least two aspects of foraging behavior. Longer tarsi may be favored among active perch-gleaning insectivores if it effectively increases the birds’ “stretch-and-pick” distance. Longer tarsi may also be selected for in insectivores that scan close, dense vegetation, regardless of prey-capture
technique. In this situation longer tarsi allow the bird to bob vertically, and search more substrates from the same perch (see Fitzpatrick 1978: fig. 12, p. 51). Among insectivorous birds such as aerial hawksers that remain for relatively long periods of time at one perch, however, shorter tarsi should be favored, as the birds center of gravity is closer to the perch, enhancing balance at the expense of maneuverability. This advantage would be expected to be important to Thamnomanes, which typically sit with a characteristic upright posture, close to the perch, much like many hawking tyrannids.

Relative tarsus length (tarsus length/cube root of body weight) is less in Thamnomanes (T. caesius, T. schistogynus, and T. ardesiacus) than in Thamnophilus (Fig. 1b; $P < 0.002$, Mann-Whitney $U$-test). Tarsus lengths of Thamnophilus and Thamnomanes are also significantly different after the effect of size is removed ($P < 0.025$, ANCOVA). The two analyses indicate that these sally-gleaning Thamnomanes have relatively shorter tarsi than do the predominately perch-gleaning Thamnophilus.

**Bill.**—A broad, flat bill is often found in species that capture much of their food on the wing (Keast 1972). Such bills typify entire families of highly aerial feeders, e.g., Apodidae and Hirundinidae. The functional importance of this bill type can be gauged by noting that it frequently
appears in species that habitually hover-glean or hawk, even though closely-related perch-gleaning species have a more typical narrow bill (e.g., Setophaga in the Parulini; Bennett 1980).

Relative bill width in antshrikes was determined for 14 species of Thamnophilus, five species of Dysithamnus, and five species of Thamnonianes (data not available for Western Antshrike [T. occidentalis]). The relative width of the gape (width of gape/culmen length) is not significantly different between Thamnonianes and a pooled sample of Thamnophilus and Dysithamnus. Bill shape nonetheless varies among antshrikes. The relative width of the bill (bill width at the nares/culmen length) is not significantly different between Thamnophilus and Dysithamnus; therefore, these two genera were pooled to compare to Thamnonianes. Relative bill width (bill width at the nares/culmen length) is greater in Thamnonianes than in Thamnophilus and Dysithamnus (Fig. 1c; \( P < 0.05 \), Mann-Whitney U-test; \( P < 0.001 \), ANCOVA).

As Fig. 1c shows, however, there is overlap between Thamnonianes and Thamnophilus plus Dysithamnus with regard to relative bill width. This overlap is due both to a narrow-billed Thamnonianes (Plumbeous Antshrike [T. plumbeus]: mean bill width ratio = 0.236, \( N = 20 \)) and to several wide-billed Dysithamnus (Spot-crowned Antvireo [D. puncticeps]: mean bill width ratio = 0.254, \( N = 20 \); Streak-crowned Antvireo [D. striaticeps]: mean bill width ratio = 0.275, \( N = 20 \)). Thamnonianes plumbeus in Venezuela forages by perch-gleaning or sallying in low mixed-species flocks in forest understory, much like D. mentalis (P. Schwartz and E. Willis, pers. comm. Willis). Dysithamnus puncticeps is reported to regularly hover-glean (Greenberg and Gradwohl 1980), and D. striaticeps, which is closely related (Cory and Hellmayr 1924) may do the same. Bill shape in insectivorous birds, however, may be influenced not only by the manner in which the prey is caught, but also by the nature of the prey itself (e.g., Greenberg 1981). A full understanding of the significance of bill shape variation in antshrikes will require more complete information of both the foraging behavior and prey of these birds.

Bristles.—Semibristles, a feather-type intermediate in structure between bristles and contour feathers (Lucas and Stettenheim 1972), are found on the face and gular region in all species of Thamnophilus, Dysithamnus, and Thamnonianes. In addition to semibristles, two species of Thamnonianes, T. caesius, and T. schistogynus, have feathers approaching the bristle grade in which the rachis clearly extends beyond the distal barbs (Fig. 4). These bristles are distributed on the lores, along the edge of the maxilla, and on the gular region. The bristles of T. schistogynus and T. caesius are often well developed and resemble the rictal bristles of tyrant flycatchers, although the rachis is less stiffened and the distal barbs
Fig. 4. Facial feathers of *Thamnomanes*: (A) rictal semibristle of *T. ardesiacus*; (B) loral bristle of *T. schistogynus*. Note the absence of distal barbs and the prominence of the rachis over the proximal barbs in the bristle of *T. schistogynus*.

are more fully developed. The remaining species of *Thamnomanes* (*T. ardesiacus*, Saturnine Antshrike [*T. saturninus*], *T. plumbeus*, and *T. occidentalis*) lack bristles, although semibristles are distributed in the same facial areas that contain bristles in *T. caesius* and *T. schistogynus*.

The function of rictal bristles has never been clear (Stettenheim 1973). They are often found in hawking or sally-gleaning birds such as tyrannids, and, thus, it has been suggested that they aid in prey capture by increasing the effective surface area of the bill, a claim that has never been substantiated. Furthermore, some birds that feed extensively on the wing, including such highly-specialized aerial feeders as the Apodidae and Hirundinidae, lack well-developed rictal bristles. Conover and Miller (1980) presented experimental evidence that the rictal bristles do not aid in food capture, but may help to protect the eyes. In this case, development of rictal bristles would still be selected for in sallying or hawking birds. Prey size might affect the development of rictal bristles, however, as birds feeding on relatively small or soft-bodied insects may not subject their eyes to as much danger as would birds feeding on larger insects.

**Systematics**

The genus *Thamnomanes* was described by Cabanis (1847) for a new species of antshrike, *T. caesius*. Historically *Thamnomanes* contained only *caesius* and its allospecies, *T. schistogynus*. Meyer de Schauensee (1966) admitted to *Thamnomanes* four additional species, *ardesiacus, saturninus, plumbeus*, and *occidentalis* (all previously considered to be *Dysithamnus*).
Meyer de Schauensee considered *ardesiacus* to be a *Thamnomanes* on the basis of unpublished observations by E. O. Willis of similarities in foraging behavior between *ardesiacus* and *caesius*; the other three species were believed to be related to *ardesiacus*, and were also transferred to *Thamnomanes*. Two questions arise from this change in taxonomy: do the behavioral similarities between *ardesiacus* and *caesius* support congeneric status? Are *ardesiacus*, *saturninus*, *plumbeus*, and *occidentalis* more closely related to *caesius* than to other antshrikes?

The foraging behavior of *caesius*, *schistogynus*, and *ardesiacus* is associated with some subtle morphological differences distinguishing these species from other antshrikes. These similarities in foraging behavior and morphology may reflect common ancestry, or may have resulted from the independent development of a similar foraging technique. Antshrikes on the whole are very similar structurally. Their differences in morphology may be related to subtle differences in foraging technique. This relationship makes it difficult or impossible to correctly reconstruct phylogenetic history from standard morphological data.

These three species also share a common plumage pattern in each sex (except for the unique female plumage of *T. schistogynus*). These plumage patterns are quite simple, however, and differ from most *Thamnophilus* and all *Dysithamnus* by the lack of wing-bars, tail-spots, tail pattern, or other distinctive features, and not by the common possession of a unique plumage pattern. A few *Thamnophilus* (e.g., Uniform Antshrike [*T. unicolor*] and Mouse-colored Antshrike [*T. murinus*] also have similar, simple plumage, thus, this character cannot be relied upon to unite *caesius*, *schistogynus*, and *ardesiacus*.

The species *ardesiacus* thus shares with members of *Thamnomanes* a specialized foraging behavior and morphology. These similarities are difficult to interpret as evidence of phylogenetic relationship. There is no evidence, however, that *ardesiacus* is more closely related to any species in *Thamnophilus*, *Dysithamnus*, or any other genus of antbird. Therefore, I recommend following Meyer de Schauensee (1966, 1970) in treating *ardesiacus* as species of *Thamnomanes* and hypothesize that the specializations for sally-gleaning exhibited by *caesius*, *schistogynus*, and *ardesiacus* evolved only once. The taxon *saturninus* was for some time thought to be a subspecies of *ardesiacus* (see Cory and Hellmayr 1924, Zimmer 1932). The two taxa have very similar plumages, are largely parapatric and resemble each other morphologically (below), all of which suggest a close relationship between these two forms. The behavior and voice of *saturninus* is also similar to that of *ardesiacus* (E. Willis, pers. comm.).

Hellmayr (*in* Cory and Hellmayr 1924) believed *plumbeus* to be related to *ardesiacus* on the basis of similarities in "proportions," "shape of the
bill,” and male plumage. The shape of the bill of plumbeus, at least in terms of relative width, is actually not similar to that of ardesiacus; rather the bill of plumbeus is significantly narrower than is the bill of ardesiacus ($P < 0.002$, Mann-Whitney $U$-test). The bill of plumbeus more closely resembles the narrow bill shape predominant in Thamnophilus and Dysithamnus than it does the relatively broad bills of caesius, schistogynus, ardesiacus and saturninus. Hellmayr did not indicate what “proportions” he considered to be similar between plumbeus and ardesiacus. Weights for plumbeus are not available, and so the morphology of parts of the body cannot be considered individually. If two structures of the body, wing length and tarsus length, are compared simultaneously, however, one can compare at least some of the “proportions” of plumbeus and ardesiacus.

Wing length and tarsus length in antshrikes are compared in Fig. 5. There is a general positive correlation between the two characters. Two groups stand out from the general pattern. The first is composed of a single species, Rufous-capped Antshrike (T. ruficapillus), which has relatively long legs and short wings. This combination suggests that ruficapillus may be particularly adept at “stretch-and-pick” perch-gleaning. Another group,
also separated from most antshrikes, is composed of several antshrikes with long wings and short tarsi. This group is composed of the sally-gleaning _colesius_, _schistogynus_, and _ardesiacus_, and also _saturninus_, strengthening the hypothesis of morphological similarity (and presumed relationship) between _saturninus_ and other species of _Thamnomanes_.

The remaining species currently assigned to _Thamnomanes_, _T. plumbeus_ and _T. occidentalis_, fit the general antshrike pattern of intermediate wings and tarsi, suggesting that they lack the morphological adaptations for sally-gleaning. There is no reason on the basis of “proportions” to consider either of these two species to be related to members of _Thamnomanes_. The only remaining character that would unite these species in _Thamnomanes_ is plumage pattern. Zimmer (1933) noted a resemblance in the male plumage between _plumbeus_ and _occidentalis_, and suggested that they were congeneric. Zimmer (1933) did not mention _ardesiacus_ in his discussion, although earlier Hellmayr (in Cory and Hellmayr 1924) had considered _plumbeus_ and _ardesiacus_ to be related because of similar male plumages. All three taxa (_ardesiacus_, _plumbeus_, and _occidentalis_) have dark gray or blackish male plumages: _plumbeus_ and _occidentalis_ differ from _ardesiacus_ by having white tips to the wing coverts. Black and gray are common colors for male antshrikes, including _Thamnophilus_ and _Dysitharnnus_, many of which also have white-spotted wing coverts. Although the male plumage of _T. plumbeus leucostictus_ resembles the male plumage of _ardesiacus_ in the common possession of a blackish throat, the male plumage of other populations of _plumbeus_ shows as much or more resemblance to some _Thamnophilus_, e.g., _murinus_, as they do to _ardesiacus_. As no unique plumage pattern is shared by _plumbeus_, _occidentalis_ and _ardesiacus_, this character again fails to provide evidence that _ardesiacus_ is related to the other two species, and I suggest that _plumbeus_ and _occidentalis_ be removed from _Thamnomanes_.

The question then becomes, what are the affinities of _plumbeus_ and _occidentalis_? Empirically, the species of _Dysitharnnus_ are separated from _Thamnophilus_ by their smaller size and slimmer (less deep) bill (Fig. 6). Neither character can be relied upon as evidence of common phylogenetic history. Nonetheless, vocal similarities among several species of _Dysitharnnus_ (mentalis, striaticeps, and puncticeps [Slud 1964]; mentalis and the Spot-breasted Antvireo [_D. stictothorax_], T. A. Parker, pers. comm.) support the hypothesis that these species are related. When bill structure of _plumbeus_ and _occidentalis_ is compared to other antshrikes, _occidentalis_ falls into the _Thamnophilus_ group. This is not surprising, as _occidentalis_ was originally described as a _Thamnophilus_ (Chapman 1923). The dimensions of the bill suggest that _plumbeus_ is a _Dysitharnnus_, although _plum-
Fig. 6. Species means of culmen length by depth of bill at the nostrils in Thamnophilus (open circles) and Dysithamnus (closed circles). The regressions are significantly different ($P < 0.001$, ANCOVA). The species occidentalis and plumbeus are represented by open and closed triangles, respectively.

beus is larger than all other Dysithamnus and is approaching a size and morphology intermediate between Dysithamnus and Thamnophilus.

SUMMARY

Most antshrikes (Formicariidae: Thamnophilus, Dysithamnus, and allies) are generalized perch-gleaning insectivores. Several species of the South American ant-shrike genus Thamnomanes, however, are characterized by a foraging behavior that appears to be unique within the family. These Thamnomanes are sally-gleaning insectivores that utilize a “sit-and-wait” foraging strategy accompanied by long prey-capture sallies. Quantitative data on some aspects of this foraging behavior are presented for two species of Thamnomanes studied in the field in Peru and Bolivia.

The morphology of Thamnomanes is predicted to show specializations reflecting their sally-gleaning behavior: sally-gleaning antshrikes are predicted to have relatively longer wings, shorter tarsi, and wider bills than perch-gleaning antshrikes. These predictions are tested using museum specimens, and the morphology of Thamnomanes is shown to fit the predictions.

The systematics of Thamnomanes is re-evaluated with special consideration given to foraging behavior and accompanying morphological specializations. The genus Thamnomanes is recommended to contain four species known or inferred to be sally-gleaners. Two species
currently classified in *Thamnomanes*, *T. plumbeus*, and *T. occidentalis*, are believed on the basis of morphology to be perch-gleaners, and are removed from the genus.

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**LITERATURE CITED**


REPRODUCTIVE BEHAVIOR AND VOCALIZATIONS
OF THE BONIN PETREL

GILBERT S. GRANT, JOHN WARHAM, TED N. PETTIT,
AND G. CAUSEY WHITTOW

The Bonin Petrel (Pterodroma hypoleuca) is an abundant, colonially-breeding seabird in the central Pacific Ocean. It breeds in winter and spring, being ashore between August and June. The population of this species in the Northwestern Hawaiian Islands exceeds one million birds; about 10,000 breed at Midway Atoll (Harrison and Hida 1980). Until recent studies of egg development and chick growth (Pettit et al. 1982a, 1982b; Grant et al. 1982) the species had been little studied (mainly because it usually digs breeding burrows in loose sand and because it nests on islands of difficult access), although some details of breeding biology had been reported (Howell and Bartholomew 1961, Woodward 1972, Amerson et al. 1974, Clapp and Wirtz 1975). This paper deals with courtship behavior, vocalizations, pre-laying activities including the pre-laying exodus, egg-laying and hatching, and incubation shifts.

METHODS

Many nest burrows on Sand Island, Midway Atoll (28°13'N, 177°23'W) in the Leeward Hawaiian Islands are excavated under lawns. Burrows may be 3 m long and over 1 m deep. The single white 39-g egg is laid in an enlarged nest chamber which is lined with grasses and needles of the ironwood tree (Casuarina equisetifolia). The structural integrity of these sites allowed repeated examination of the same nests throughout the breeding season.

Vertical shafts 15–20 cm in diameter were dug to the nest chambers. The shafts were covered with plywood and the nests inspected during the pre-laying, incubation, and nestling periods—almost daily from 30 December 1979–25 March 1980 and from 10 December 1980–23 May 1981. Small sticks were placed across burrow entrances to detect nocturnal visits. If the fences were disturbed the nest contents were checked. “Nest-days” refers to the number of nests examined multiplied by the number of days checked.

Behavioral observations were made at dusk and after dark with the aid of street lights, moonlight, and partly obscured flashlights. We detected no differences in behavior of petrels nesting under dim street lighting and those in unlit areas. Recordings of vocalizations made with a Uher 4000 IC machine using a Nagamichi CM 300 microphone and a tape speed of 19 cm/sec were analyzed with a Kay 6061B Sona-Graph. Most behavioral observations and vocalizations were recorded in December and early January, prior to egg-laying.

Times referred to here are local. The time of sunset was obtained from the U.S. Navy Meteorological Station on Midway Atoll. Color-marked birds were sexed by assuming that a bird on top during copulation was male. Where appropriate, means are given ± one standard error.

STUDY AREA

Much of Sand Island is covered with buildings, runways, and roads. The major petrel nesting colonies and the relative burrow densities are indicated in Fig. 1. Very few Bonin
Petrels breed on Eastern Island, Midway Atoll, due to the very dense rat populations (Grant et al. 1981). The largest petrel colonies on Sand Island are on the man-made hills near the harbor, under the *Casuarina* trees and on the fringes of the golf course, near the chapel and school, the area stretching northwest from the hangar to the dunes, and in Area 7 (a restricted zone). The Area 7 and golf course colonies support substantial Wedge-tailed Shearwater (*Puffinus pacificus*) nesting populations during the summer. The larger shearwater often evicts and may kill Bonin Petrel chicks when it takes over and enlarges the petrel burrow for its own use. Laysan Albatrosses (*Diomedea immutabilis*) nest on the surface of the ground above the petrel burrows in most areas but we saw little interaction between the albatrosses and petrels. The only impact of this association occurs when young albatross chicks occasionally become stuck in petrel burrow entrances. Typically the chick, if tightly wedged in the entrance, dies and blocks the passage of the petrels. We saw this happen only about 10 times during the course of our study.

**NIGHTLY ARRIVAL**

Bonin Petrels are strictly nocturnal in their activities over land. During 36 nights between 8 December 1980 and 28 January 1981, the first birds appeared overhead 13.2 ± 1.3 min after sunset, range 11 min before sunset–26 min after sunset. Only three birds, however, appeared before sunset, all under dark, rainy skies with 100% cloud cover. In general, the lighter the sky and the less the cloud cover, the later the time of arrival.

The first birds overhead at dusk flew quite high. As the light faded their
numbers increased, and aerial pursuits with their associated chattering cries were heard. Soon many were circling just above the tops of the *Casuarina* trees and before long some were skimming the ground, particularly in open places near the burrowed areas; 15–25 min after the first high-flying birds had appeared, some had alighted, the earliest before the last daylight had gone.

On the Snares Islands, New Zealand, Mottled Petrels (*Pterodroma inexpectata*) (Warham et al. 1977) tended to arrive later with respect to sunset than did Bonin Petrels on Midway; but skuas (*Catharacta skua*) kill petrels at the Snares Islands whereas there is no natural predator on Midway Atoll.

**BURROW EXCAVATION**

Burrows in hard substrate were used year after year while those dug in loose coral sand frequently collapsed between breeding seasons. Bonin Petrels returned to Midway and nearby islands in August and September (Woodward 1972, Amerson et al. 1974, Clapp and Wirtz 1975) and began excavating new burrows or cleaning out old ones. When we arrived in early November digging had begun; some burrows were nearly completed but digging continued well into the laying period. Late season digging may have been done by prospecting pre-breeders or failed breeders. Both members of a pair dug. They picked with their bills to loosen the soil and then kicked it backwards with their webbed feet. The wrists and the unused foot supported the bird while the other foot kicked back the sand. Up to 3.3 kicks/sec were given and the ejected sand thrown 0.3–1.0 m beyond the burrow entrance. The bird typically kicked a few times with one leg, then a few times with the other, and so on.

In three instances, burrows were lengthened apparently because of our daily checks of burrow occupancy. The earlier lining was buried in these nests and the burrows were extended up to 0.4 m. The nest-chambers were relined 4–11 days later. Lengthening of the burrow in response to human disturbance has also been reported in Leach’s Storm-Petrel (*Oceanodroma leucorhoa*) (Gross 1935) and in Wedge-tailed Shearwaters (Shallenberger 1973).

Burrow entrances were often packed with vegetation both before and during incubation. The bird at the burrow entrance tugged and tore at grass stems and tossed them over its shoulder or packed them around the opening. The result was an eliptical hole about 10 × 7 cm through which the petrel had to squeeze to enter and leave. Nest blocking has been reported in several other petrels (e.g., Warham 1958, 1960, 1967; Warham et al. 1977; Bartle 1968). Bartle (1968) suggested that nest blocking disguised the burrow from predators and Warham (1960) thought it might be related to a preference for darkness while on land. *Pterodroma hypoleuca*
may block the larger shearwater burrows so that they match their own smaller profiles.

**OLFACTION**

We were struck by the frequency of the “beak to the ground” posture when Bonin Petrels were near their burrows. Sand removed from burrows was “investigated” by the petrels who adopted this posture. Crude experiments indicated that olfaction may play a role here. On 14 December 1981 Warham placed both fists on the ground about 0.6 m apart, upwind of a pair of excavating birds. Both petrels ceased activities at their nest entrance and walked 1 m from the petrel burrow entrance, nibbled his fingers and investigated his notebook with the “beak to the ground” posture. He had handled another petrel extensively an hour earlier. The next night Grant repeated this experiment by handling a petrel (over 30 m from the experimental site) with his left hand only. He knelt down 2 m upwind from a burrow entrance where the male was digging and the female was below. The male immediately stopped and walked toward his right hand but then turned toward his left hand which the male nibbled (ignoring his right one). From this crude experiment, we suggest that olfaction is useful near the burrow entrance but not inside as the birds accepted domestic chicken (*Gallus gallus*) and other petrel eggs placed in the nest. This experiment extends the use of chemical communication by procellariiform birds (Wenzel 1980).

**LOCOMOTION NEAR THE NESTING AREAS**

Some petrels landed in open spaces and then walked to their nests where these were under trees, but the canopy was open enough to allow many to land through the trees at their burrows. Birds usually landed 3–7 m from burrows. They walked easily with a rather rolling gait, holding their bodies low and horizontal, head and neck outstretched and wings folded to the body. They pushed their way through patches of low grass but then often paused to lift their heads and view their surroundings. Some clambered onto low sloping fallen limbs and perched there. Occasionally a bird was seen climbing the vertical trunk of a *Casuarina* even though it could fly from unobstructed ground with ease, even in calms, in contrast with other *Pterodroma*, particularly larger members of the genus, and some shearwaters, which appear to need a sharp descent in which to gain air speed.

**TERRITORIAL ACTIVITY**

Much of the behavior of grounded birds apparently concerned the defense of a territory around a burrow entrance. Some birds patrolled an area within 2–3 m of their burrow entrances. Intruders were repelled by
sudden dashes with outstretched wings. Most intruders shifted quickly, sometimes flicking up, part flying, part jumping, to alight a few meters away. Many repulsions occurred without vocalizations, but often loud *kik-oo-o-er* calls caused some nearby petrels to scatter without any direct attack. Such calls tended to be contagious; presumably other territory-holders were responding. Some fights occurred; the birds spread their wings and pecked hard at each other's napes and heads. No injuries were known to have resulted. One bird entered a burrow *churring* loudly, continued this while briefly underground and then emerged, still calling, to chase away a nearby petrel which fled after responding with harsh cries.

**SEXUAL ACTIVITY**

Particularly in the pre-laying period of December and early January pairs were often seen with one bird walking close on the tail of another and reaching toward it. Such pairs tended to wander within a restricted area (in one instance within no more than a square meter) and their peregrinations were interspersed with quiet periods during which the pursuer preened the head and neck of the other. Some preening was so vigorous that the recipient drew back as if to disengage, but without actually doing so. Mutual allopreening also occurred, sometimes with the presumed female turning her beak to preen her partner's throat. These activities preceded copulation. In two instances, the leading birds gave a harsh *kuk-ku-er* at intervals and the followers gave a low rather continuous purring and churring sound (see below) during which the caller's throat pulsated. These same birds also used a higher pitched version of the other's call: *kik-oo-o-er*, as described below. In both of these episodes the pursuer was on top of the pursued during mounting so it seems that the harsh *kuk-ku-er* was given by the female, the *churr* and the higher pitched call by the male. While it was usually the follower that *churred*, sometimes the leading bird did so when a silent pursuer trailed. As individual birds were not studied in earlier breeding seasons, it was not possible to determine if the petrels observed had been paired with each other the previous season or were prospecting for mates.

Nine pairs of Bonin Petrels were seen copulating on the ground between 10 and 21 December 1980. On 10 December a marked pair copulated at 20:28 and again at 20:45; the male attempted unsuccessfully to mount at 20:38. Copulation by this same pair was also seen at 19:19 on 11 December. With two marked pairs, copulation took place on the ground within 2 m of the mouths of their burrows.

During copulation the female swayed her head from side-to-side while
the male nibbled with his bill at her crown and cheeks, shifting his at-

tentions from one side of her face to the other. The birds were silent during
copulation. The wings of the male were fluttered once to maintain balance
during mounting and the female partly opened her wings to rest the wrists
on the ground and moved her feet to keep her position. After cloacal
contact was attained and the male had stopped thrusting, the female turned
and gently nibbled his breast feathers. The male then dismounted. Cop-
ulation episodes lasted from 20 sec to 4–5 min.

In one instance post-copulatory behavior consisted of mutual preening
of bills and faces. In another, the female walked to the burrow and began
digging within a minute of the male’s dismounting, leaving the male to
preen himself.

AERIAL ACTIVITY

Bonin Petrels have a low wing loading (33N/m²) (Warham 1977) and
are very maneuverable birds. Their maneuverability was well shown by
the frequent aerial chases 2–3 m above ground around small salients <8
m across at the edges of the belts of trees. The birds touched down gently
and took off with equal facility without a headwind.

Before the pre-laying exodus, aerial activity involving the repeated cir-
cling of petrels above the colonies formed a major feature of their behavior.
Immediately after dark, the noise of their callings was considerable, but
tended to fade as the night advanced and more birds were on the ground.
In the air the most discernible interactions were the high-speed pursuits
of one bird by another. Typically, with many birds in the air, two would
suddenly converge and for a few seconds one would chase hard on the tail
of the other, both calling briefly. Longer chases also developed. Although
no bird was individually recognizable, some of the aerial activity could be
followed in the illumination provided by street lights. For example, single
birds on the ground flew up and circled repeatedly a restricted area before
alighting near their take-off point or close to another bird with whom they
might display. We gained no evidence that birds calling in the air evoked
vocal response from those on the ground or vice versa. Much of the be-

davior described may have been performed by pre- and failed breeders.

Petrels in flight may become disoriented by mercury and sodium vapor
street lights or other sources of artificial lighting. Such disorientations may
result in collisions with trees, buildings, or other objects; injuries sustained
in this manner are not uncommon. The effect of artificial lighting upon
fledging petrels is not known but high density of lights is the worst hazard
to fledglings of Newell’s Shearwater (Puffinus puffinus newelli) on the is-
land of Kauai (Telfer 1979). Individual shearwaters and petrels may be
brought down to the ground by following a bird in flight with a high-intensity light beam. Warham (pers. obs.) used similar techniques successfully in obtaining petrels in flight in the Southern Hemisphere.

VOCALIZATIONS

Most of the calls were of short duration; prolonged duetting as occurs with shearwaters (pers. obs.) was not noted. All appeared to be given on expiration of breath unlike those of some other petrel groups, e.g., Diomedea and Puffinus, whose vocalizations are given both on inspiration and expiration.

Calls of grounded birds.—There was much variation in the tempo, structure, and pitch among the calls given by different birds (Fig. 2 [1–9]), and some of this variation was so extreme that certain calls could not be categorized. Many were also incomplete; only one or two syllables of a trisyllabic call were used—a kuk or a ti-ti—but we have concentrated here on fully developed vocalizations used by actively courting or threatening petrels. Many called in response to play-back of their calls but these responses were only brief. Most recordings were made with the microphone less than 2 m from birds that were often literally at our feet. The most recognizable calls were as follows:

(1.) A harsh, raucous cry, phonetically kuk-u-er, and often rising abruptly in pitch at the end. This call usually lasted 0.5–0.9 sec, occasionally as long as 1.1 sec, and was often preceded by a short burst of kuks, and such calls or kuk-ers were often interspersed among the more extended trisyllabic utterances. Most of these harsh cries consisted of almost unstructured noise with the main frequency between 1 and 4 kHz. Call (B) of the spectrograms of Fig. 2(1, 2) show typical examples.

Such calls were usually repeated only two or three times during one song burst, but occasionally were repeated seven or eight times. During repetition the structure of each phrase might change. Fig. 2(8A, 8B) shows two harsh kuk-u-er given by the same bird during a single burst of song. The longer call was the last of a short series and shows how the mainly unstructured and “noisy” vocalization can be modified into a more harmonic one. Despite the harmonics, the second call still sounded raucous and unmusical, the harmonics were only 300–350 Hz apart and were typical of the harmonic pattern of this type of call.

(2.) A high-pitched call made up of a series of 3–8 staccato syllables uttered in rapid succession (Fig. 2[4]). This loud chattering sound was roughly transcribed as ti-ti-ti . . . or kik-kik-kik . . . . There are four clearly defined harmonics reaching to 6 or 7 kHz, hence the high pitch and more piping character than the generally rasping and lower pitched kuk-u-er. Each ti is a simple noise-free cry (Davis 1964). As with the kuk-u-er
Fig. 2. Calls of grounded Bonin Petrels. (1) Part of duet: the *churr* of (A) stopped when its partner gave the hoarse *kuk-u-er* cry (B). (2) Two courting birds: (A) giving a harsh *kuk-u-er* with little pattern to the sound, and (B) a clearer, high-pitched *kik-ooo-er* with strong harmonics about 1 kHz apart. (3) Duetting: a *churring* bird call (A) overlaps with its partner’s low pitched *kuk-u-er* call which was similar in form but of lower pitch than that of the bird in (1) above. (4) A *churr* and staccato *ti-ti-ti* . . . given by a lone bird. (5) A duet between a *churring* bird (A) and one (B) using the harsh *kuk-u-er*. (6) Part of a series of very low-pitched cooing cries from a bird underground. (7) Part of a series of gasping whimpers from a bird in a burrow, pitched at less than 1 kHz. (8) Development of the *kuk-u-er* call: phrase (B) followed (A). Note that the harmonics in (B) are only about 350 Hz apart. (9) Duetting: one bird (A) gives a harsh *kuk-u-er* and the other (B) gives a single and then a series of *ti* calls.
these notes could develop into longer more complex calls like those of the second series in Fig. 2(9B). Such calls sounded like clearer and higher-pitched versions of the *kuk-u-er* cry and were written down as *kik-ooo-er*. A more extreme example is shown in the analysis of Fig. 2(2B) where a simple abrupt *ti* or *kik* is expanded into a raucous high-pitched cackle.

The main frequency in this class of calls was between 4 and 7 kHz, with the harmonics well separated by 1.0–1.5 kHz, quite different from harmonics, if any, of the *kuk-u-ers*.

(3). The *churr* (Fig. 2[1A, 3A, 4, 5A]) is a quiet, very low-pitched call made up of a broad band of sound between 0.5 and 1.0 kHz. It was sometimes sustained at constant volume for 4–6 sec, but punctuated by silences of 0.3–0.5 sec long. Although the *churr* often sounded like a low, continuous growl, not all birds called alike; some had a more crackling quality. The sonograms mostly showed a broad, unstructured band of noise, e.g., in Fig. 2(5A), but sometimes a pulsed pattern was clearly audible (Fig. 3[1]). Indeed the field description of this call as a *churr* or *purr* implies a pulsed structure and other calls of this nature that appeared to be only noise proved to be a series of regular pulses. An example is given in Fig. 3(2)—note the rapid changes of amplitude with time. Fig. 3(3) provides a different example of a *churr*, one seemingly composed of a series of very close, slightly modulated harmonics. Wide band and amplitude analyses showed that this too had a structure of short and regular pulses of sound. The pulse rates in the examples analyzed varied from 78–190 pulses/sec and the *churrs* with the lower rates of pulse were those whose rhythmic character was clear to the unaided ear.

(4.) Miscellaneous calls. Birds in burrows and on the ground also used a variety of quiet chitterings, whistles and whimpers. These were imperceptible except at very close range, but were easily recorded, particularly when the birds were underground. Fig. 2(6) shows two calls from a series of very low pitched cooing cries and Fig. 2(7), part of a long series of even lower pitched calls, was described as “gasping whimpers.” These calls were apparently only given when two birds were together.

(5.) Duets. By watching and recording duettists it was found that one used the harsh *kuk-u-er* and the other used the higher pitched chattering cry or its extended equivalent Fig. 2(2, 9). Two duettists never used the same type of song. Duets also occurred with one bird *churring* and the other giving the low *kuk-u-er* (Fig. 2[1, 5]). In the first the *churring* bird did not fall silent until after its partner responded—a sequence noted repeatedly; the *churring* bird abruptly stopped when its partner began.

Birds that *churred* could also switch to the *ti-ti-ti* call like the solo birds of Figs. 2(4) and 3(3). *Churring* birds did not use the hoarse *kuk-u-er*. These observations support the hypothesis confirmed by watching vocal-
Fig. 3. Analyses of Bonin Petrel calls using an extended time scale. (1) Top: a churr analysed at half speed and (bottom) tape played at normal speed. Middle spectrograph used a narrow band filter, upper one a wide band filter; both show that call was composed of a series of rather regular pulses. (2) Part of an analysis of the churr of Fig. 2(4) slowed down four times. The amplitude trace (top) and the wide band analysis (bottom) emphasize the pulsed character of this call. (3) Bottom: a slowed down churr followed by two ti-ti calls from the same bird. The churr seems to be based on a series of very close harmonics (narrow band analysis) but the broad band and amplitude traces above show that the call is made from very fine pulses. (4) The low aerial moan of Fig. 4(3) is also composed of a rapid succession of pulsed sounds.
izing birds that eventually copulated, that the birds using the *churr* and the *ti-ti-ti* sequence are males, the others female.

**Calls from flying birds.**—It was difficult to get clear records of aerial song (Fig. 4[1–8]), but by placing the microphone about 2 m high and pointing vertically, lone and dual-flying petrels were recorded as they passed within 5 m. During aerial chases, both chased and chaser called but we could not see which bird gave which call. Most close flying lasted only 1–4 sec and the duets were likewise brief. Essentially, the calls given in flight were the same as those used on the ground, but were Doppler shifted when recorded, e.g., Fig. 4(2).

The harsh *kuk-u-er* calls (e.g., Fig. 4[1, 7]) have sonagrams similar to those of such calls from grounded birds (c.f. Fig. 4[1, 4, 7] with Fig. 2[1, 2, 9]). Both are made from broad bands of noise with underlying bands of close harmonics in some individuals (Fig. 4[4]). Some such calls were preceded by short pulses or *kiks* as shown in that figure.

The *ti-ti-ti* call as delivered in flight had clear, well-separated harmonics and a high pitch (Fig. 4[2]). These calls were far-carrying and were largely responsible for the overall chattering character of the aerial chorus. The development of the *ti-ti-ti* sequence appeared to be related to the intensity of the pursuit and some quite complex vocalizations resulted, e.g., Fig. 4(5, 8).

The third common call was a low, coarse, slurred moan lasting 2–3 sec, ending quite abruptly; most of the sound lay just below 1 kHz (Fig. 4[3]). The call has obvious similarities with the *churr* (Fig. 2[4]), but to our ears this aerial call did not have the pulsed structure revealed with finer analysis. This is shown by the sonagram and amplitude trace of the slurred aerial call of Fig. 4(3), re-analyzed in Fig. 3(4). Presumably the slurred effect is a consequence of the rapid movement of the calling bird and the inability of our ears to detect the underlying pulsations.

The details of the aerial duets showed their affinity with duets of grounded birds. Typically one of the pair used the moan and the high-pitched *ti-ti-ti* or its variants, the other the hoarse *kuk-u-ers* (Fig. 4[6]). In Fig. 4(7), about 100 msec after the moaning bird stopped, the other responded with a loud *kuk-u-er*. The high pitched chatter of the *ti-ti-ti* aerial cry was often described as *wik-wik-wik* . . . in field notes, and toward the end it was often drawn out into a loud crowing squeal, much as in the ground call analyzed in Fig. 2(2).

Most aerial chases involved birds that used the moan and the *ti-ti-ti* . . . call and its many variations; they were the chasers and the others with their deeper voices, the chased. We concluded, based on call groups, that the males were the chasers and the females, the chased.
Fig. 4. Calls of Bonin Petrels in flight. (1) Two successive, deep harsh *kurr* calls from the same bird, variants of the trisyllabic *kuk-u-er* cry. (2) A succession of chattering *ti-ti-ti* calls from a bird flying past the microphone; the main energy was at about 5 kHz. (3) The low, coarse, slurred moan; note trace of a harmonic at about 5 kHz. For magnified analysis of this call see Fig. 3(4). (4) A harsh *kuk-u-er* preceded by three staccato *kus*. (5) An elaboration of the chattering *ti-ti* call. (6) Duet with one bird using a harsh low-pitched call (A), the other an elaboration of the *ti-ti* sequence (B). (7) Duetists: the bird using the low moan fell silent and its partner gave a loud *kuk-u-er* about 100 ms later. (8) An elaboration of the chattering *ti-ti* call.
We noted a great deal of intraspecific variation in calls. This presumably helps in individual recognition in nocturnal species such as the Bonin Petrel where visual cues are limited or non-existent.

**BREEDING**

*Pre-laying period.*—Bonin Petrels lined their nests with bits of grass and *Casuarina* needles 36.0 ± 2.7 days (N = 6) before the egg was laid. One nest (not included in the above) was found already lined 48 days before the egg appeared. The lining was generally added in one night (N = 5), but in one case the lining was begun on one night and completed on the following one.

Twenty-three nests were checked daily for a total of 930 “nest-days” before laying, to establish occupancy by day. The burrows were empty on 847 nest-days (91%) and occupied by at least one petrel on 83 (9%) nest-days—the earliest time of daytime occupancy prior to laying was 48 days. Both members of a pair were present on only 19 of the 83 occupied nest-days, i.e., only 2% of the total nest-days. Four burrows (17%) held no petrel by day before egg-laying, the mean number of consecutive days on which no petrels were present being 39.0 days, range 29–48. Fourteen burrows (61%) never had two petrels present during the daytime, while in one burrow both members of pair were present on 7 days (during one consecutive 4-day and another consecutive 3-day period). Before egg-laying, daytime occupancy by other *Pterodroma* was infrequent (Warham 1967, Harris 1970, Warham et al. 1977).

Thirty petrel nests were checked in the morning, by fencing over the burrow openings to determine the frequency of nocturnal visits before laying. Nightly visits declined from ca. 80%–ca. 10% (Fig. 5) during the pre-laying exodus. The maximum pre-laying exodus interval recorded was 24 days (nest #70 of Fig. 6). Intact fences showed that nothing had entered the burrow during the night. Displaced sticks provided less certain information because sticks were shifted by rats, by Laysan Albatrosses stumbling into them, and by other petrels. One Bonin Petrel briefly entered four different burrows within 10 min during the pre-laying period. Many of the visits shown in Fig. 6, immediately before egg-laying, were probably made by rats or by birds other than the owners. However, in four instances marked birds were present in the burrows 2–3 days (N = 2), 1 day (N = 1), and on the eighth day (N = 1) before the egg was laid. In six nests (Fig. 6) lack of disturbance the day before egg-laying indicates that both sexes had left (nest chambers were inspected and found to be empty).

Thus, some Bonin Petrels exhibited a marked pre-laying exodus of up to 24 days while others occasionally returned to the nest in the 2 weeks before laying. Copulation was seen on the ground near burrows on the
nights of 10–21 December, 21 or more days before the first egg was laid. We were unable to follow successfully a marked pair of petrels from copulation to egg-laying. Warham et al. (1977) found that the pre-laying exodus in *P. inexpectata* lasted from 9 to at least 16 days while Imber (1976) suggested the pre-laying absence by females may average 60 days in *P. macroptera gouldi*.

**Egg-laying.**—In 1980 the mean egg-laying was 27.2 January ± 0.5 days (range 13 January–7 February); 92% of the eggs were laid in a 13-day period (Fig. 7A). In 1981 the mean egg-laying date was 27.1 January ± 0.8 days (range 11 January–11 February), but only 81% of the eggs were laid in a 13-day period.

No evidence of relaying was found. Some eggs were collected on the day of laying for physiological measurements and many were lost to rats during incubation. Twenty-nine burrows where eggs were lost between 16 January and 15 March were checked on several occasions in February, March, April, and May for the presence of a new egg. In only one instance was a second egg found, and this was laid 2 days after the first was collected. Because yolk formation requires 15 or more days in the Bonin Petrel (Grau et al., unpubl.) this egg was laid by another female. In three nests a second egg appeared during incubation alongside the first but one of them was invariably buried in the burrow within a few days. Egg neglect occurred, though rarely (Grant et al. 1981), and thus the second egg was probably laid by another female during a temporary absence by the "owners." Bonin Petrels that had lost an egg visited their burrows up to 40–50

![Fig. 5. Visitation rates of Bonin Petrels to 30 burrows before egg-laying. Regression line is fitted by least squares (r = 0.888, N = 20 days).](image)
days after their loss. If an egg was then laid by another female during an absence of the original owners, we hypothesize the returning original pair might evict the newcomers and incubate the egg, thus appearing to have renested.

Incubation.—The incubation period averaged 48.7 days (Grant et al. 1982) and consisted of several alternating spans or bouts of incubation by both members of the pair. Incubation spans were short during egg-laying (1–3 days, $\bar{x} = 2.0 \pm 0.3$ days, N = 9) and later they were longer (2–15 days, $\bar{x} = 8.8 \pm 0.7$ days, N = 22). The average of 31 spans was $6.8 \pm 0.8$ days. Incubation duties were shared almost equally by both sexes, assuming that the first short bout associated with egg-laying was by the female. Data from the subsequent two spans at six nests were used to calculate the roles of the sexes in incubation. Long bouts averaged $8.3 \pm 1.3$ days for males and $7.0 \pm 1.0$ for females. On only 1 of 245 nest-days during the incubation period were both members of the pair in the burrow during the day.

Hatching.—The mean hatching date was 11.6 March $\pm 1.0$ days in 1980 and 17.9 March $\pm 1.7$ days in 1981 (Fig. 7B). The difference between the mean laying and mean hatching period gives an incubation period of 44.4
days in 1980 and 49.8 days in 1981, not substantially different from the 48.7 days (Grant et al. 1982) actually measured.

Hatching success was greatly affected by rats (Rattus sp.). In 1980 at the chapel colony only 1 of 26 eggs hatched; the remainder were taken by rats. In the nearby school colony, however, 19 of the 21 eggs laid subsequently hatched and the two which did not were broken by petrels (Grant et al. 1981). In 1981 no eggs hatched in the chapel colony and rats took some eggs in the school colony. Of 44 nests monitored, 21 (48%) eggs subsequently hatched. Losses were due to: rat predation—20% (N = 9);
crushing by petrels—7% (N = 3); desertion—5% (N = 2); eggs being ad-dled—5% (N = 2); burial in nest by petrels—2% (N = 1); burrow cave-in caused by people—2% (N = 1); burrow cave-in—2% (N = 1). The cause of 9% (N = 4) of nest-losses was unknown. All 14 chicks examined daily in 1981 during the nestling period survived a minimum of 62 days. At least five of these fledged (R. Shea, pers. comm.).

SUMMARY

Observations on Bonin Petrels (Pterodroma hypoyleuca) breeding on Sand Island, Midway Atoll, Northwestern Hawaiian Islands were made in 1979–80 and 1980–81. At Midway, many pairs were observed on the ground with the help of street lighting.

The birds’ behavior and locomotion, their courtship, copulation, and territorial activity are described. Aerial activity included high-speed dual flights with loud calls. These and the calls of grounded birds are described.

Petrels lined their nest chambers about 36 days before the single egg was laid and there was a pre-laying exodus of up to 24 days. The mean laying date was 27.2 January and the eggs hatched, on average, 48.7 days after incubation began. Both sexes incubated in alternating spans of about 6.8 days. Mean hatching dates were 11.6 March 1980 and 17.9 March 1981. Due to differential rat predation, hatching success varied between colonies and from one year to the next.

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LITERATURE CITED


NESTING BIOLOGY OF LAUGHING GULLS IN RELATION TO AGRICULTURAL CHEMICALS IN SOUTH TEXAS, 1978–81

DONALD H. WHITE, CHRISTINE A. MITCHELL, AND RICHARD M. PROUTY

Various aspects of the breeding biology of Laughing Gulls (Larus atricilla) have been studied extensively in Florida (Dinsmore and Schreiber 1974, Schreiber et al. 1979, Schreiber and Schreiber 1980), New Jersey (Bongiorno 1970, Burger and Beer 1976, Burger 1976, Montevecchi 1978), and Massachusetts (Noble and Wurm 1943), but little is known of their yearly fledging success in Texas or elsewhere. The Laughing Gull is a common colonial nester along most of the Texas coast, second only to the Cattle Egret (Bubulcus ibis) in breeding abundance; however, the Laughing Gull may be threatened in Texas because of suspected declines at certain traditional nesting locales (Blacklock et al. 1979). Since Laughing Gulls often nest in proximity to agricultural and industrial areas, we were concerned that environmental pollutants might be adversely affecting productivity. In 1978–1981 we conducted studies along the south Texas coast to learn more about the nesting ecology of Laughing Gulls and to evaluate the effects of environmental contaminants on reproduction.

STUDY AREAS AND METHODS

Our study areas were located at Corpus Christi, Nueces Co., (27°52'N, 97°30'W), Port Mansfield, Willacy Co., (26°14'N, 97°26'W), and Laguna Vista, Cameron Co., (26°06'N, 97°18'W), Texas, encompassing a 200-km stretch of the south Texas coast (Fig. 1). At these sites, Laughing Gulls nested on unnamed, dredged material islands 1–2 ha in size made of oyster shell and sand. About 50–75% of the island surfaces were covered by patches of low vegetation (<1 m) dominated by sea oxeye (Borrichia frutescens), coast bacopa (Bacopa monnieri), and glasswort (Salicornia spp.). The study island in Nueces Bay at Corpus Christi was flanked by industries on the south shore of the bay and by agricultural lands on the north shore; the one at Port Mansfield was located in the Laguna Madre, 0.8 km from the outlets of two major agricultural drains. The Laguna Vista island was about 20 km south of where the Arroyo Colorado, a major waterway that traverses the heavily farmed Rio Grande Valley, empties into the Laguna Madre.

In 1978, we studied Laughing Gulls only at Corpus Christi, expanding our studies in 1979–1981 to include Port Mansfield and Laguna Vista. We made approximate biweekly visits to nesting islands beginning in late January through mid-April each year. Thereafter study sites were visited once a week, usually on the same day. We began marking nests with numbered stakes when eggs first appeared in nests. We staked the first 60–75 nests receiving eggs each year at Corpus Christi and Laguna Vista; all nests were staked at Port Mansfield. Nest marking usually was completed within a 2-week period. Eggs within nests were marked with the assigned nest number and the egg sequence number when known. During weekly visits we collected data on the fate of eggs and young at marked nests; also, we counted all
Fig. 1. Laughing Gull study-sites on the south Texas coast.
unmarked nests with eggs as an indicator of colony size. We were only able to keep an accurate account of chicks in marked nests up to about 1 week posthatch; after that, some chicks would depart the nest and hide in surrounding vegetation when we drew near. Chicks found dead each week were removed from the islands. As the chicks approached fledging (flying age), they would gather at the ends of the small islands away from us. By carefully searching the vegetation for chicks as we proceeded through the colony each week and then counting those chicks at the ends of the islands, we were able to estimate overall productivity for the colony (fledglings/total nests) at each locality. Chick counts ceased once young were observed flying. Although some degree of asynchrony existed, most chicks reached fledging age within a 2-week period. Only marked nests were used in estimating clutch-size, hatching success, and fate of chicks to 1 week; total nests were used in estimating fledging success on a colony basis.

At the initiation of egg-laying each year we collected one fresh egg from each of 201 unmarked nests on islands adjacent (usually <1 km) to study sites for organochlorine residue analyses. Also, intact eggs that failed to hatch in marked nests were analyzed to determine if residues were implicated in egg failure. The chemical analyses were conducted at the Patuxent Wildlife Research Center following the methods described by Clark et al. (1983). Quantification limits were 0.1 ppm for organochlorine pesticides and 0.5 ppm for polychlorinated biphenyls (PCBs) on a wet weight basis. Residues in 5% of the samples were confirmed by mass spectrometry. To determine if shell thinning had occurred, we compared eggshell thicknesses of the eggs we collected with those of eggs collected in Texas in the 1920s before the pesticide era and now housed at the Welder Wildlife Foundation, Sinton, Texas. Eggshells were measured with a micrometer to the nearest 0.01 mm.

RESULTS AND DISCUSSION

Nesting chronology and colony size.—The colonies studied were known to exist at least since 1973 (Texas Colonial Waterbird Society 1982). Colony size was fairly consistent during our study among years; the average number of breeding pairs on study islands was 200 at Corpus Christi, 53 at Port Mansfield, and 220 at Laguna Vista. Laughing Gulls are permanent residents in coastal Texas, but are not always associated with the breeding islands (Burger and Beer 1976). Toward the end of January each year a few gulls (usually <20) were seen loafing on study islands. Most were in winter plumage; only 2% had black heads. By mid-February, about 25% of the nesting population had gathered on the islands and some pairs were seen standing on the island interiors. By mid-March, 50–75% of the expected breeders had gathered on the islands and courtship activity had begun in earnest; 95% of the gulls had black heads but less than 20% had red bills. By the time egg-laying began in late April, all adults had bright red bills. We never saw immature-plumaged birds breeding and none were seen around the nesting islands after about mid-April.

Nest-building began each year around the third week in April at Corpus Christi and Laguna Vista but did not commence until the last week of April at Port Mansfield. Almost all the nests were built directly on the ground adjacent to surrounding vegetation, unlike Laughing Gulls in New
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(Jersey salt marshes which nest primarily on mats in tall grass (Montevecchi 1978). Nest material in this study consisted mostly of dead stems of sea oxeye and saltbush (*Baccharis* spp.), although a few nests contained green pieces of glasswort and coast bacopa. Nests usually were well constructed, averaging about 5 cm high × 8 cm wide. Egg-laying in Texas did not begin until construction of nests was well along and almost all the nests received at least one egg. In contrast, Laughing Gulls in Florida (Schreiber et al. 1979) and New Jersey (Burger 1976) laid eggs in nests in various stages of completion and birds in New Jersey continually added nest material throughout incubation. In the Florida study, 14% of the nests initiated did not receive eggs and nests never contained green material.

The initiation of egg-laying was consistent at our study sites among years, as shown for other populations (Montevecchi et al. 1979), but the timing varied somewhat among sites. The average dates on which females laid first eggs were 21 April at Laguna Vista (N = 209), 26 April at Corpus Christi (N = 264), and 6 May at Port Mansfield (N = 157). Montevecchi et al. (1979) demonstrated a latitudinal gradient where Laughing Gulls at higher latitudes laid first eggs later; birds in Massachusetts began laying on 21–31 May, in New Jersey on 18 May, and in Florida on 15–20 April. Our data do not fit this pattern; Texas birds, nesting at a somewhat lower latitude than Florida birds, tended to lay later than Florida birds.

Hatching peaked toward the end of May at Corpus Christi and Laguna Vista, and in early June at Port Mansfield. By the first 2 weeks in July, most chicks could fly considerable distances, indicating that fledging occurred at about 5–6 weeks after hatching. The mean fledging age of Laughing Gull chicks in Florida was 42.5 days, ranging from 35–50 days (Schreiber and Schreiber 1980). After chicks fledged in Texas, they remained on the nesting islands for 3–5 weeks, usually loafing in large groups on the shores of the islands. Most of the adults also were present but by mid-August few birds of any age were associated with the nesting islands.

**Productivity.**—Nest success (fledglings/total eggs) or productivity (fledglings/total nests) for each of the three study areas is presented in Tables 1, 2, and 3. Clutch-size varied significantly (ANOVA, F = 3.7; df = 3, 160; P < 0.05) at Corpus Christi among years, ranging from 2.4–2.8 (Table 1). Sixty-five percent (N = 172) of our staked nests there had three-egg clutches, 30% (N = 78) had two-egg clutches, and 5% (N = 14) had one-egg clutches. Clutch-size at Port Mansfield was consistent (P > 0.05) among years (Table 2) and the overall average was significantly lower (t = 5.07, df = 541, P < 0.01) than at the other two sites because of a larger proportion ($\chi^2 = 22.56$, df = 1, $P < 0.01$) of two-egg clutches. Forty-six percent (N = 73) of our staked nests at Port Mansfield had three-egg clutches, 46% (N = 73) had two-egg clutches, and 8% (N = 9) had one-egg clutches.

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<td>54</td>
</tr>
<tr>
<td>Eggs hatched/nest</td>
<td>1.8</td>
<td>2.1</td>
<td>0.1</td>
<td>1.7</td>
<td>1.4</td>
</tr>
<tr>
<td>Nest success (%)</td>
<td>26</td>
<td>18</td>
<td>0</td>
<td>58</td>
<td>23</td>
</tr>
<tr>
<td>Fledglings/total nests</td>
<td>0.7</td>
<td>0.5</td>
<td>0</td>
<td>1.4</td>
<td>0.6</td>
</tr>
</tbody>
</table>

* Percentage nests that hatched at least one young.

At Laguna Vista, we found no difference ($P > 0.05$) in clutch-size among years (Table 3) but the proportion of three-egg clutches was greater ($\chi^2 = 17.32, df = 1, P < 0.01$) than at the other two sites; 75% (N = 157) of our nests there had three eggs, 22% (N = 46) had two eggs, and 3% (N = 5) had one egg. Since birds nested earlier on the average at Laguna Vista, more three-egg clutches may reflect a larger proportion of older birds nesting there. Schreiber et al. (1979) reported clutch-size of 2.8 and 2.5 in 1975 and 1976, respectively, for a Laughing Gull colony in Florida, with a higher proportion of two-egg clutches occurring in 1976 (43%) than in 1975 (15%). Most of our females laid three eggs, as seen by the mode for each year among sites (Tables 1, 2, 3), but at Port Mansfield in 1980, 59% of the females laid only two eggs. Egg loss due to depredation of eggs probably did not affect clutch-size, although we saw Laughing Gulls peck a few eggs during our visits. Undoubtedly some eggs and chicks were lost to predators, such as Black-crowned Night-Herons (*Nycticorax nycticorax*) which nested on some of the islands, but we never saw evidence of mammalian or reptilian predators. Nevertheless, egg depredation could have been missed since we visited colonies only once a week. Our estimates of clutch-size, however, compare favorably with that of Schreiber et al. (1979) who reported only minor depredation of Laughing Gull eggs.

Hatching success (eggs hatched/total eggs) at marked nests varied significantly ($\chi^2 = 101, df = 2, P < 0.01$) among locations, ranging from 4–82% at sites among years (Tables 1, 2, 3). High storm tides were responsible for the 4% success rate recorded at Corpus Christi in 1980; on 19
Laughing Gull Productivity at Port Mansfield, 1979–1981

<table>
<thead>
<tr>
<th>Parameter</th>
<th>1979 (N = 51)</th>
<th>1980 (N = 51)</th>
<th>1981 (N = 55)</th>
<th>Total (N = 157)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Clutch-size</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.4</td>
<td>2.3</td>
<td>2.4</td>
<td>2.4</td>
</tr>
<tr>
<td>Mode</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Range</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
</tr>
<tr>
<td><strong>Survival rates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% successful nests(^a)</td>
<td>84</td>
<td>76</td>
<td>89</td>
<td>83</td>
</tr>
<tr>
<td>% eggs hatched</td>
<td>63</td>
<td>52</td>
<td>71</td>
<td>63</td>
</tr>
<tr>
<td>Eggs hatched/nest</td>
<td>1.5</td>
<td>1.2</td>
<td>1.7</td>
<td>1.5</td>
</tr>
<tr>
<td>Nest success (%)(^b)</td>
<td>50</td>
<td>30</td>
<td>54</td>
<td>46</td>
</tr>
<tr>
<td>Fledglings/total nests</td>
<td>1.2</td>
<td>0.7</td>
<td>1.3</td>
<td>1.1</td>
</tr>
</tbody>
</table>

\(^a\) Percentage nests that hatched at least one young.

\(^b\) Fledglings/total eggs.

May, 95% of our staked nests were inundated and destroyed. Flooding of nests in Texas is rare and is not a continuing problem because of the low tide fluctuations and the fact that Laughing Gulls usually nest well above the high tide mark. In contrast, flooding of nests in New Jersey was the greatest source of nesting failure (Montevecchi 1978). Success at Port Mansfield was reduced in 1979 and 1980 (Table 2) probably due to poor hatchability; 20% (1979) and 22% (1980) of the eggs incubated failed to hatch. This category accounted for only 6% of the egg loss at the other two sites for all years combined, (excluding the 1980 Corpus Christi flooding). An average of 3% of the eggs at all sites (N = 630 nests) disappeared during incubation and 13% of the eggs disappeared during the hatching period; their fate is unknown. Only 1% of the eggs were found outside the nests abandoned or depredated. The overall hatching success for two-egg clutches (63%) was significantly lower ($\chi^2 = 16.49$, df = 1, $P < 0.01$), than for three-egg clutches (74%). Hatching success of Laughing Gulls in Florida in 1975 was higher in two-egg clutches (93%) than in three-egg clutches (78%), but the reverse (71% vs 87%) was true in 1976 (Schreiber et al. 1979). In studies with Herring Gulls (Larus argentatus), hatching success was lower in two-egg clutches (50%) than in three-egg clutches (72%) (Brown 1967). In our study, there was a significant relationship between average clutch-size and hatching success (Spearman's rank correlation, $r = .71$, df = 8, $P < 0.05$); as clutch-size at the various sites among years increased, so did hatching success.

Except for the flooded colony at Corpus Christi in 1980, most of the
Laughing Gull pairs each year were able to hatch at least one egg (Tables 1, 2, 3). Laguna Vista birds were especially prolific, with 96% of the nests being successful (Table 3). Although infrequent, nest abandonment was the major cause of the reduction in successful nests, especially at Port Mansfield (Table 2). Consequently, the percentage of successful nests at locations differed significantly ($\chi^2 = 60.04$, df = 2, $P < 0.01$). Clutch-size had no significant effect ($P > 0.05$) on hatching success, for 89% of two-egg nests hatched at least one young compared to 93% of three-egg nests. Since one-egg clutches were rare (6%), they were excluded from the analysis. Schreiber et al. (1979) reported that 65% of two-egg nests within an enclosure were successful compared to 88% of three-egg clutches.

Fledging success (fledglings/total nests) on a colony basis was highly variable, ranging from 0–1.6 fledglings per nest (Tables 1, 2, 3) and averaging 1.0 fledgling per nest. Except for 1981, productivity was consistently low at Corpus Christi. In 1978, about 25% of the chicks, ranging in age from a few days to several weeks, and over 100 adults at the Corpus Christi site died within a 3-day period from exposure to parathion, an organophosphate (OP) insecticide used on nearby cotton fields (White et al. 1979). Certain of the OPs are extremely toxic to wildlife for short periods after application and the number of reports of mortality in exposed avian populations has increased in recent years (Mendelssohn and Paz 1977, Zinkl et al. 1978, Stone 1979, White et al. 1979, White et al. 1982b). The adults had gathered poisoned insects from the sprayed fields and fed them to their young. In addition, many chicks probably died from star-
vation or exposure as a result of the death or inattentiveness of their parents (White et al. 1983). Again in 1979, a large number of chicks of varying age died over a several-week period at Corpus Christi, reducing productivity to only 0.5 fledglings per nest (Table 1). Because of the necrotic condition of the carcasses, we were unable to determine the cause of mortality, but OP insecticide poisoning was suspected since OPs were used heavily in the area. In a series of brain assays from chicks found dead on nearby islands, acetylcholinesterase (AChE) levels were inhibited up to 98%, indicating death from an OP insecticide. OPs kill primarily by inhibiting AChE in the nervous system, thereby disrupting synaptic transmission of nerve impulses (Hill and Fleming 1982). None of the chicks fledged at the Corpus Christi colony in 1980 where flooding occurred although 7% of the nests hatched at least one young (Table 1). Fifty-three pairs renested there and 42% of them were successful, but at one-week posthatch there were only 0.08 live chicks per nest and none fledged.

Fledging success was similar each year at Port Mansfield and Laguna Vista (Tables 2, 3), but fewer young fledged in 1980 at both colonies than in 1979 or 1981. Poor hatching success (52%) was the major cause of nest failure at Port Mansfield (Table 2) in 1980. However, about 33% of the chicks at Laguna Vista that year died from suspected OP poisoning. Brain AChE activity in a sample of the dead birds was greatly inhibited, indicating exposure to an OP compound, and inhibition was enough to account for death (>50%) in all instances (Ludke et al. 1975). The gastrointestinal tracts of the dead birds were empty, thereby negating our efforts to identify the causative agent in stomach contents. However, discussion with local landowners and pesticide applicators revealed that EPN, an OP insecticide, was being used extensively on cotton crops in the area. EPN is representative of a group of OPs that causes delayed neurotoxicity in birds (Francis et al. 1980, Ohkawa et al. 1980). Delayed mortality could have accounted for the empty stomachs in the dead birds, since the digestion process would have continued in sick birds that were unable to feed. We do not believe that the chicks starved to death since AChE activity was greatly depressed. Food restriction did not alter brain AChE activity in lab studies with chickens (Brust et al. 1971).

Overall, Laughing Gull pairs in Texas fledged 1.0 young per nest for a nest success rate of 39%. The 4-year average of 1.0 fledging per nest was below what Laughing Gulls are capable of attaining; in 5 of 10 colony attempts pairs produced an average of 1.4 fledglings per nest. Schreiber et al. (1979) reported productivity similar to our overall estimate for Florida birds within an enclosure; their colony produced flying young from 41% of the total eggs laid, or 1.1 fledglings per total nests. We know of no other published accounts of productivity in Laughing Gulls. Although human
Table 4
Organochlorine Residues (PPM, Wet Weight) in Laughing Gull Eggs from the Texas Coast

<table>
<thead>
<tr>
<th>Location</th>
<th>DDE</th>
<th>Dieldrin</th>
<th>PCBs</th>
<th>Heptachlor epoxide</th>
<th>Toxaphene</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corpus Christi</td>
<td>1.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.08</td>
<td>2.0</td>
<td>0.2</td>
<td>0.06</td>
</tr>
<tr>
<td>1978–1981 (92)</td>
<td>(92)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>(31)</td>
<td>(74)</td>
<td>(30)</td>
<td>(10)</td>
</tr>
<tr>
<td></td>
<td>0.3–91&lt;sup&gt;c&lt;/sup&gt;</td>
<td>ND&lt;sup&gt;d&lt;/sup&gt;–1.0</td>
<td>ND–14</td>
<td>ND–0.7</td>
<td>ND–1.2</td>
</tr>
<tr>
<td>Port Mansfield</td>
<td>3.7</td>
<td>0.06</td>
<td>1.0</td>
<td>0.06</td>
<td>0.2</td>
</tr>
<tr>
<td>1979–1981 (56)</td>
<td>(56)</td>
<td>(7)</td>
<td>(47)</td>
<td>(2)</td>
<td>(15)</td>
</tr>
<tr>
<td></td>
<td>0.8–63</td>
<td>ND–0.9</td>
<td>ND–6</td>
<td>ND–0.3</td>
<td>ND–2.2</td>
</tr>
<tr>
<td>Laguna Vista</td>
<td>1.3</td>
<td>0.05</td>
<td>2.0</td>
<td>0.03</td>
<td>0.06</td>
</tr>
<tr>
<td>1979–1981 (53)</td>
<td>(53)</td>
<td>(3)</td>
<td>(50)</td>
<td>(2)</td>
<td>(6)</td>
</tr>
<tr>
<td></td>
<td>0.3–47</td>
<td>ND–0.5</td>
<td>ND–10</td>
<td>ND–0.7</td>
<td>ND–0.6</td>
</tr>
</tbody>
</table>

* Geometric mean.
*<sup>b</sup> Number of eggs containing detectable residues.
*<sup>c</sup> Range.
*<sup>d</sup> ND = not detected.

disturbance can adversely affect reproduction, especially in the pre-egg and incubation stages (Schreiber 1979), we do not believe that our weekly visits were detrimental. In fact, we observed that Laughing Gulls in Texas were reluctant to flush from their nests until we had approached within 5–10 m. Most birds quickly returned to their nests or chicks after we had left the immediate area. Also, egg depredation by Laughing Gulls was rare during our visits and we never saw gulls or any other birds take chicks.

Organochlorine residues and shell thickness.—Of 201 eggs analyzed for organochlorine pesticides and polychlorinated biphenyls (PCBs) during the 4-year period, all contained detectable residues of DDE (the major metabolite of DDT), ranging from 0.3–91 ppm wet weight (Table 4). In addition, 85% of the eggs contained PCBs, ranging from 0.5–14 ppm, but dieldrin, heptachlor epoxide, and toxaphene were detected less frequently and residues were low, seldom exceeding 1 ppm for any of these compounds.

Except for a 39% decrease between 1978 and 1979 at Corpus Christi, geometric mean levels of DDE in eggs remained relatively unchanged at sites among years, although the high extremes detected in individual eggs each year varied greatly. DDE means were highest (ANOVA, $F = 3.8$; df = 2, 198; $P < 0.05$) in eggs at Port Mansfield, perhaps reflecting their location near the outlets of two major agricultural drains (Fig. 1). DDE residues in Laughing Gull eggs were low since only 3% of the eggs contained >10 ppm DDE. Eggs that failed to hatch were no higher ($P > 0.05$) in DDE residues than were fresh ones, indicating that DDE probably had
little effect on hatchability. Lipid content of eggs averaged 9.7 ± 0.4%, but was not significantly correlated ($P > 0.05$) with DDE residues. Eggshell thinning was detected at all colonies, ranging from 7–14%, but we found no significant relationship ($P > 0.05$) between eggshell thickness and log DDE residues in eggs. In addition, there was no significant relationship ($P > 0.05$) between percentage shell thinning and hatching success. PCBs, dieldrin, heptachlor epoxide, and toxaphene residues were far below known-effect levels (Stickel 1973, 1975) and are not suspected of causing reproductive problems. Roseate Spoonbills (Ajaia ajaja) had good reproduction in Texas with pollutant levels similar to what we report here for Laughing Gulls (White et al. 1982a).

CONCLUSIONS

Our data indicate that exposure to highly toxic OP insecticides, such as parathion and EPN, may impair reproduction in Laughing Gulls. During three of four breeding seasons, OP compounds were implicated in mortality that reduced fledging success by as much as 33%. The adults were attracted to recently-sprayed fields, possibly even keying on spray planes, as a readily obtainable source of dead and dying insects. One farmer in 1978 reported dead adults in his cotton fields shortly after the crops had received a parathion treatment; he observed the birds hawking insects over the fields and foraging between the rows even as the spray was being applied. On many occasions we have seen Laughing Gulls and swallows (Hirundinidae) hawking insects over cotton fields but we have no prior knowledge of pesticide use on these areas. Unfortunately, chick stage in the gull colonies usually coincides with the time of peak spraying in the cotton fields, thereby exposing the chicks to poisoned food items brought by the parents.

It is difficult to assess whether or not 1.0 fledgling per nest is adequate to maintain a stable population, not only from a logistics standpoint, but also because of a scarcity of reproductive data on this species. Recent censuses have indicated that Laughing Gull numbers in Texas have remained stable (Texas Colonial Waterbird Society 1982), but the use of highly toxic OP compounds on agricultural crops near the breeding colonies may pose serious threats to the population. We recommend that less toxic materials to birds, such as malathion (Hill et al. 1975), be used on crops in areas where breeding colonies occur and that spraying be delayed, when feasible, until the chicks have fledged.

SUMMARY

Laughing Gulls (Larus atricilla) were studied along the south Texas coast during 1978–1981 to determine productivity and to evaluate the effects of environmental pollutants on
reproduction. The average clutch-size was 2.6, ranging from 2.3–2.8. Sixty-six percent of
the eggs hatched and 82% of the pairs hatched at least one egg. Productivity (fledglings/total
nests) averaged 1.0 fledgling per nest. DDE and other organochlorine residues were low in
eggs (usually <3 ppm wet weight) and were not suspected of causing reproductive problems.
However, organophosphate pesticides sprayed on crops near the study areas reduced pro-
ductivity by as much as 33% during 3 of 4 years, implying that certain of these chemicals
may pose serious threats to the population.

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U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Gulf Coast Field Station, P.O. Box 2506, Victoria, Texas 77902 (DHW, CAM); Patuxent Wildlife Research Center, Laurel, Maryland 20708 (RMP). (Present address DHW: U.S. Fish and Wildlife Service, School of Forest Resources, Univ. Georgia, Athens, Georgia 30602.) Accepted 20 Apr. 1983.
CHARACTERISTICS OF SUPERNORMAL RING-BILLED GULL CLUTCHES AND THEIR ATTENDING ADULTS

GLEN A. FOX AND DORA BOERSMA

Recent reports of female-female pairing and/or polygyny in Western Gulls (Larus occidentalis) (Hunt and Hunt 1977), Ring-billed Gulls (L. delawarensis) (Conover et al. 1979a, Ryder and Somppi 1979), California Gulls (L. californicus) (Conover et al. 1979a), and Herring Gulls (L. argentatus) (Shugart and Southern 1977, Fitch 1979, Shugart 1980), indicate plasticity in the mating systems of larids. Such plasticity may allow individuals to adjust to changing ecological constraints. Certain behaviors are adaptive in one situation but not another and mating systems of local populations of the same species may vary in different environmental or density situations (Emlen and Oring 1977).

In mate selection, any given female will choose from the subset of available mates she contacts during the appropriate, critical time period (Gladstone 1979). If a female recruit, “divorcee,” or recent “widow” does not encounter any available territory-holding males, or cannot satisfactorily compete with older, more experienced, or more dominant females, she may be excluded from forming a heterosexual pair-bond. However, extra-pair copulations have been observed in gulls (Goethe 1937, Hunt and Hunt 1977, Conover et al. 1979a), thus providing an alternative possibility for unmated females. The recipient of an extra-pair copulation (i.e., the female) needs assistance to provide adequate parental care and to minimize her energy expenditure. Females who co-operate and form an association with another female increase their reproductive experience (if they can find space to nest) and increase their fitness if young are raised. This would be adaptive under ecological conditions which bias the operational sex ratio (the ratio of sexually active males to fertilizable females [Emlen and Oring 1977]) in favor of females.

In recent years there has been a very marked expansion in the range and numbers of the Ring-billed Gull (Ludwig 1974, Conover et al. 1979b). It is in areas of range expansion and growing colonies that supernormal clutches (N ≥ 5 eggs) now occur. Supernormal clutches are frequently attended by two females (Conover et al. 1979a, Ryder and Somppi 1979, Kovacs-Nunan 1982) suggesting anomalies in the operational sex ratio. Such anomalies in the sex ratio have been documented in the Western Gull and Herring Gull (Burger and Gochfeld 1981). In this paper we report the incidence, composition and fertility of supernormal Ring-billed Gull
clutches in a large, relatively stable colony, and the sex and plumage characteristics of attending adults.

METHODS

Supernormal (five- and six-egg) clutches observed in a colony of approximately 27,500 pairs (Blokpoel 1977, pers. comm.) on Gull Island, near Brighton, Ontario (43°50'N, 77°40'W), were marked with wooden stakes on 6 May 1980. Additional supernormal clutches were marked when found. In the course of our studies, the island was searched thoroughly and repeatedly, thus, the chances of our having missed any clutches are minimal. An attempt was made to trap attending adults at the nest, using the drop trap of Mills and Ryder (1979). All trapped individuals were banded with a USFWS aluminum band. Trapping efforts stopped when we captured two individuals from any one site; thus, we unfortunately did not allow for the possibility of a third attending bird (and hence the possibility of polygyny). However, we did check for the presence of unbanded individuals whenever we approached these nests and none were observed. Birds were sexed by bill measurements (Ryder 1978) and four individuals (two pairs) were collected to confirm the predicted sex by gonadal inspection. We classified each bird into one of two plumage types. It was considered a subadult if it possessed a subterminal tail-band or remnants thereof, buffy wing coverts, or had less than two white “windows” on the primaries. Adults were as described by Ludwig (1974). We have rarely observed gulls with a subterminal tail-band as well as “windows” in their primaries.

The length and maximum width of eggs were measured with vernier calipers. Eggs were opened near the end of the incubation period, checked for visible embryonic development, and the approximate age of the embryos recorded (Ryder and Somppi 1977). Obvious differences in background color and/or size of eggs within a clutch were recorded as an indication of the possibility that two females had contributed to the clutch, as there is generally a greater variability in egg size and background color among different Herring Gull clutches than within the same clutch (Baerends and Hogan-Warburg 1982). Where possible the supernormal clutches were subdivided into constituent clutches on the basis of similarity of background coloration and/or size. Eggs missing at the time of measuring were classified as of “unknown” fertility. In 1979, we trapped the attending adults on five supernormal clutches and opened the eggs.

RESULTS

Twenty-one supernormal clutches (0.08%, based on an estimated population of 27,500 pairs) were found on Gull Island, Lake Ontario, in 1980. Embryonic age determinations suggested the majority (74%) were completed during the last week in April and the first week of May, corresponding to what appeared to be the peak of clutch completions in the colony.

In 14 of 21 supernormal clutches (66.6%) there were obvious differences in egg background color and/or size (Table 1). At five of these nests we were able to trap only one individual; thus, the sex of only 37 attending adults was determined. Eight (38.1%) of the supernormal clutches were attended by a male and at least one female. In three of these eight clutches there were differences in coloration and/or size suggesting the possibility of more than one female contributor (i.e., polygyny or nest parasitism)
Table 1
Sex and Plumage Characteristics of Ring-billed Gulls Trapped on Supernormal Clutches, Gull Island, 1980, in Relation to Clutch-size and Apparent Fertility

<table>
<thead>
<tr>
<th>Nest</th>
<th>Clutch composition(^{a})</th>
<th>Fertility(^{b})</th>
<th>Sex</th>
<th>Plumage type</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2 + 3</td>
<td>2 + 3</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>2</td>
<td>2 + 3</td>
<td>2 + 3</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>3 + 2U</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>4</td>
<td>2 + 3</td>
<td>5</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>5</td>
<td>M, F</td>
<td>SAd, SAd</td>
</tr>
<tr>
<td>6</td>
<td>5</td>
<td>5</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>7</td>
<td>5</td>
<td>5</td>
<td>M, F</td>
<td>SAd, SAd</td>
</tr>
<tr>
<td>8</td>
<td>6</td>
<td>5 + 1U</td>
<td>M, F</td>
<td>Ad, Ad</td>
</tr>
</tbody>
</table>

38F, 3U (92.7\%)\(^{c}\)

<table>
<thead>
<tr>
<th>Nest</th>
<th>Clutch composition(^{a})</th>
<th>Fertility(^{b})</th>
<th>Sex</th>
<th>Plumage type</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>4 + 1</td>
<td>(3 + 1U) + 1</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
<tr>
<td>10</td>
<td>2 + 3</td>
<td>2 + (2 + 1U)</td>
<td>F, F</td>
<td>SAd, SAd</td>
</tr>
<tr>
<td>11</td>
<td>2 + 3</td>
<td>2 + 3</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
<tr>
<td>12</td>
<td>2 + 3</td>
<td>(2 + 1I)(1 + 1I)</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
<tr>
<td>13</td>
<td>6</td>
<td>3 + 2I + 1U</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
<tr>
<td>14</td>
<td>3 + 3</td>
<td>3 + (2 + 1I)</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
<tr>
<td>15</td>
<td>3 + 3</td>
<td>3I + 3I</td>
<td>F, F</td>
<td>Ad, Ad</td>
</tr>
<tr>
<td>16</td>
<td>3 + 3</td>
<td>3 + 3I</td>
<td>F, F</td>
<td>Ad, SAd</td>
</tr>
</tbody>
</table>

27F, 14I, 3U (61\%)\(^{d}\)

<table>
<thead>
<tr>
<th>Nest</th>
<th>Clutch composition(^{a})</th>
<th>Fertility(^{b})</th>
<th>Sex</th>
<th>Plumage type</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>2 + 3</td>
<td>(1 + 1U) + (2 + 1I)</td>
<td>F, —</td>
<td>Ad, —</td>
</tr>
<tr>
<td>18</td>
<td>5</td>
<td>5</td>
<td>F, —</td>
<td>Ad, —</td>
</tr>
<tr>
<td>19</td>
<td>2 + 3(^{c})</td>
<td>(1 + 2U) + (2 + 1I)</td>
<td>F, —</td>
<td>Ad, —</td>
</tr>
<tr>
<td>20</td>
<td>3 + 3</td>
<td>3 + 3</td>
<td>F, —</td>
<td>Ad, —</td>
</tr>
<tr>
<td>21</td>
<td>3 + 3(^{c})</td>
<td>(2 + 1U)(1 + 2U)</td>
<td>F, —</td>
<td>Ad, —</td>
</tr>
</tbody>
</table>

20, 2I, 6U (71\%)\(^{d}\)

\(^{a}\) Grouping of eggs based on differences in coloration and/or measurements.

\(^{b}\) Eggs are fertile unless noted otherwise: 1 = infertile, U = unknown.

\(^{c}\) Total fertile (F), infertile (I) and unknown (U) minimum fertility.

\(^{d}\) Failed to trap "mate."

| Grouping of eggs based on differences in coloration and/or measurements. | Eggs are fertile unless noted otherwise: 1 = infertile, U = unknown. | Total fertile (F), infertile (I) and unknown (U) minimum fertility. | Failed to trap "mate."

\(^{c}\) One egg missing; given fate U.

We trapped two females at eight and single females at the remaining five supernormal clutches (Table 1) in contrast to a total of 25 males and 15 females trapped at 40 three-egg clutches in this colony during the same period \(\chi^2 = 13.115, \text{df} = 1, P < 0.001\). All five individuals trapped on supernormal clutches in this colony in 1979 were females in contrast to 11 of 20 attending two- and three-egg clutches \(P < 0.01\), Fisher’s Exact Probability Test).

On the basis of our criteria six of eight of the heterosexual associations were comprised of individuals in adult plumage. In one instance two females attending a supernormal clutch were in adult plumage (Table 1). In
six others, one female was adult and the other subadult, and in one instance both females were in subadult plumage (Table 1). The difference in frequency of pairs with both plumage types between heterosexual associations and apparent female-female associations is significant ($P < 0.03$, Fisher’s Exact Probability Test).

Based on eggs with embryonic development (minimum fertility estimate), supernormal clutches with a male in attendance had a higher minimum fertility (92.7%) than those at which no male was trapped (65.3%) ($\chi^2 = 18.53$, df = 1, $P < 0.001$) (Table 1). Of 25 eggs examined from supernormal clutches in this colony in 1979, a minimum of 16 (64%) was fertile and a minimum of five (20%) was infertile.

On 20 May 1980, a female (765–99332) in adult plumage attending a clutch of five eggs $(3 + 2)$ was trapped on Gull Island. Another female (765–99335) was trapped on the same clutch on 24 May. Two eggs were infertile and the remainder addled. The nest was deserted by 27 May. On 12 June 1980, female 765–99332 was trapped on a clutch of four eggs $(2 + 2)$ in the colony on the Eastern Headland, Toronto Outer Harbour (43°30'N, 79°22'W). Her “mate” was unbanded and could not be trapped but appeared to be a female (P. M. Fetterolf, G. Tessier, and H. Blokpoel, pers. comm.). Hence, female 765–99332 was a member of two distinct cooperative nesting associations in a single season, separated temporally by a maximum of 23 days and spatially by a distance of 142 km.

DISCUSSION

Supernormal clutches have been mentioned in the Ring-billed Gull literature as early as 1941 and apparently occur throughout much of its present range (Table 2). The majority of supernormal clutches in this study were produced during the peak of egg-laying suggesting that they were not the result of “last resort” reproductive attempts nor that the behaviors by which they arose are only adopted by those females who arrive after the peak of clutch completion or who lose their mate after laying. Kovacs and Ryder (1981) have recently reported that some female-female associations are maintained for two successive years and that they show nest-site fidelity. Supernormal clutches are frequently attended by two females (this study, Conover et al. 1979a, Ryder and Somppi 1979) and in our study 50% of these females were in subadult plumage. If these subadult-plumaged females are indeed younger, they can increase their reproductive experience as a member of a female-female association and may thus enhance reproductive success in subsequent years. One female was a member of two female-female associations separated temporally and spatially within one breeding season.

Conover et al. (1979a) reported a polygynous group of three females and
Table 2

Variation in Calculated Prevalence of Five- and Six-egg Ring-billed Gull Clutches in Colonies with Portion of Range, Growth Status, Size, and Time

<table>
<thead>
<tr>
<th>Portion of range</th>
<th>Colony location</th>
<th>Growth</th>
<th>Year</th>
<th>Size</th>
<th>Prevalence per 1000 nests</th>
<th>Source*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long established</td>
<td>Miquelon Lake, Alta.</td>
<td>STBL^a</td>
<td>1965</td>
<td>435</td>
<td>2.3</td>
<td>(1)</td>
</tr>
<tr>
<td></td>
<td>Lozinsky’s Slough, Sask.</td>
<td>STBL</td>
<td>1958</td>
<td>1200</td>
<td>1.7</td>
<td>(2)</td>
</tr>
<tr>
<td></td>
<td>Bachelor’s Is., Man.</td>
<td>STBL</td>
<td>1979</td>
<td>1596</td>
<td>5.6</td>
<td>(3)</td>
</tr>
<tr>
<td></td>
<td>Rogers City, L. Huron</td>
<td>STBL</td>
<td>1979</td>
<td>8000</td>
<td>3.0</td>
<td>(4)</td>
</tr>
<tr>
<td></td>
<td>Mohawk Is., L. Erie</td>
<td>DECN^b</td>
<td>1972</td>
<td>1000</td>
<td>5.7</td>
<td>(5)</td>
</tr>
<tr>
<td></td>
<td>Muggs Is., L. Ont.</td>
<td>INCR^c</td>
<td>1972</td>
<td>2375</td>
<td>19.0</td>
<td>(5)</td>
</tr>
<tr>
<td></td>
<td>Gull Island, L. Ont.</td>
<td>SAT'D</td>
<td>1980</td>
<td>6069</td>
<td>0.5</td>
<td>(6)</td>
</tr>
<tr>
<td>Eastern Headland, L. Ont.</td>
<td>Lawrence R.</td>
<td>INCR</td>
<td>1980</td>
<td>68,000</td>
<td>1.0</td>
<td>(6)</td>
</tr>
<tr>
<td>Expansion</td>
<td>Honey Lake, Calif.</td>
<td>INCR</td>
<td>1941</td>
<td>75</td>
<td>26.7</td>
<td>(9)</td>
</tr>
<tr>
<td></td>
<td>Banks Lake, Wash.</td>
<td>INCR</td>
<td>1953</td>
<td>717</td>
<td>34.9</td>
<td>(10)</td>
</tr>
<tr>
<td></td>
<td>Sprague Lake, Wash.</td>
<td>INCR</td>
<td>1978</td>
<td>2700</td>
<td>16.1</td>
<td>(11)</td>
</tr>
<tr>
<td></td>
<td>Potholes Reservoir, Wash.</td>
<td>DECN</td>
<td>1978</td>
<td>850</td>
<td>18.0</td>
<td>(11)</td>
</tr>
<tr>
<td></td>
<td>Okanagan Lake, B.C.</td>
<td>INCR</td>
<td>1972</td>
<td>11,000</td>
<td>1.9</td>
<td>(11)</td>
</tr>
<tr>
<td></td>
<td>Vrooman Is., L. Superior</td>
<td>INCR</td>
<td>1979</td>
<td>167</td>
<td>305.4</td>
<td>(13)</td>
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<tr>
<td></td>
<td>Gravel Is., L. Superior</td>
<td>SAT'D</td>
<td>1979</td>
<td>378</td>
<td>5.3</td>
<td>(14)</td>
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<tr>
<td></td>
<td>Granite Is., L. Superior</td>
<td>INCR</td>
<td>1977</td>
<td>1600</td>
<td>121.0</td>
<td>(15)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>INCR</td>
<td>1979</td>
<td>2400</td>
<td>41.0</td>
<td>(16)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>INCR</td>
<td>1980</td>
<td>2699</td>
<td>28.0</td>
<td>(16)</td>
</tr>
</tbody>
</table>

* Stable.
^a Declining.
^c Increasing.
^d Saturated.

* (1) Vermeer (1970); (2) G. A. Fox (unpubl.); (3) Koonz (1980); (4) Wm. Southern (pers. comm.); (5) R. D. Morris (pers. comm.); (6) P. M. Fetterolf, G. D. Tessier and H. Blokpoel (pers. comm.); (7) this study; (8) Lagranda and Mousseau (1981); (9) Moffitt (1942); (10) Johnston and Foster (1954); (11) Conover et al. (1979a, 1979b); (12) Merilees (1974); (13) Blokpoel et al. (1980); (14) J. P. Ryder (pers. comm.); (15) Somppi (1978b); (16) Kovacs-Nunan (1982).

a single male attending a supernormal clutch in a single nest bowl. Hence, our male-attended supernormal clutches may represent the products of polygynous groups although we did not observe any unbanded individuals incubating these clutches during casual observations. The eggs differed in size and/or coloration in only 37% of the male-attended superclutches and five-egg clutches were more frequent than six (Table 1). This suggests that a single female may have produced some of these supernormal clutches. We know of no documentation of a female Ring-billed Gull laying five eggs. However, Parsons (1976) has shown that 79% of 102 pairs of Herring
Gulls in a continuous laying experiment laid five or more eggs. Nest parasitism, which would also artificially increase clutch-size, has been observed in Ring-billed Gulls (D. Boersma, unpubl.). However, this mechanism is more likely to account for four-egg clutches than five- or six-egg clutches since the latter imply multiple acts of parasitism.

Minimum fertility of supernormal clutches ranged from 61–93% depending whether or not a male was in attendance. Other investigations have reported minimum fertilities of 60–75% in supernormal clutches of this species attended by female-female associations (Conover et al. 1979a, Ryder and Somppi 1979). These fertility rates are relatively high and do not differ from the average hatching success of normal clutches. This may reflect the fact that individuals of this species frequently nest at very high densities which may provide increased opportunity for fertilization through extra-pair copulations.

No data on the relative philopatry of the sexes have been published for this species. In Herring Gulls, the male is the more philopatric sex (Chabrzyn and Coulson 1976). Thus, in new or rapidly growing colonies, the majority of the immigrants will be female and often young (Kadlec and Drury 1968). On this basis, we would predict, in areas of range expansion, a greater prevalence of female-female associations and polygyny in small growing colonies than in large, possibly saturated, or declining colonies where an abundance of both sexes might be expected. A review of the available data supports this hypothesis (Table 2). The prevalence in colonies in the long-established range (median = 2.65/1000) is markedly lower than in those in areas of range expansion (median = 28.0/1000, \( U = 14, P < 0.01 \)). The prevalence in growing colonies (median = 27.35/1000) is significantly higher than that in stable colonies (median = 2.65/1000, \( U = 4, P < 0.01 \)) and declining or saturated colonies (median = 1.9/1000, \( U = 30, P < 0.01 \)). This suggests that Ring-billed Gull supernormal clutches result from behavioral responses to a skewed operational sex ratio accompanying range expansion and/or colonization.

**SUMMARY**

Some Ring-billed Gull (Larus delawarensis) clutches of five and six eggs in the Gull Island colony in Lake Ontario in 1980 were attended by at least two females while others were attended by at least one male and one female. Since we did not ascertain whether or not a third individual was in attendance, we can only conclude that these supernormal clutches resulted from active female-female associations, polygyny, or from a single female. The female-female associations frequently involved one individual in subadult plumage. One female was a member of two consecutive female-female associations at two different colonies in the same breeding season. Minimum fertility of supernormal clutches was higher in those with a male in attendance. The prevalence of supernormal clutches is higher in growing colonies and in areas of range expansion than in saturated and declining colonies or in colonies...
within the long-established range. This suggests that supernormal clutches result from behavioral responses to a skewed operational sex ratio that accompanies range expansion and colonization.

ACKNOWLEDGMENTS

We gratefully acknowledge the field assistance of L. Armour, J. Ellenton, D. Jeffrey, M. McPherson, and J. Struger. H. Blokpoel, P. M. Fetterolf, K. Kovacs-Nunan, R. D. Morris, J. P. Ryder, P. L. Ryder, and G. D. Tessier provided data for other colonies without which our thesis would have been greatly weakened. We thank C. Matheson, Ontario Ministry of Natural Resources, and his staff at Presqu'ile Provincial Park, for permission to work on Gull Island. G. R. Bortolotti, H. Blokpoel, J. Chardine, M. Erwin, A. J. Gaston, K. Kovacs-Nunan, P. Mineau, R. D. Morris, J. P. Ryder, P. L. Ryder, W. E. Southern, and D. V. Weseloh provided constructive comments on earlier drafts of this manuscript.

LITERATURE CITED


CANADIAN WILDLIFE SERVICE, NATIONAL WILDLIFE RESEARCH CENTRE, OTTAWA, ONTARIO K1A 0E7, CANADA. ACCEPTED 2 APR. 1983.

COLOR PLATE

The colorplate frontispiece of Bluish-slate Antshrike (Thamnomanes schistogynus) has been made possible by an endowment established by George Miksch Sutton (1898-1982). Painting by F. P. Bennett, Jr.
EFFECTS OF PARASITIC FLIES (*PROTOCALLIPHORA* SPP.) ON NESTLINGS OF MOUNTAIN AND CHESTNUT-BACKED CHICKADEES

CLIFFORD S. GOLD AND DONALD L. DAHLSTEN

*Protocalliphora* (Diptera: Calliphoridae) larvae are hematophagous parasites which attack the nestlings of a broad range of nidicolous birds. The genus is widespread geographically and is found in many habitats. Despite the fact that nest infestations are common, only limited biological information and even less quantitative information exists on these flies. In part this can be attributed to difficulties and limitations imposed by working in active nests without undue disturbance of the birds and to the lack of success of rearing the flies in a laboratory situation.

During the course of a long-term study on the population biology of Chestnut-backed (*Parus rufescens*) and Mountain (*Parus gambeli*) chickadees we have noted that most nests were infested by *Protocalliphora* and that these infestations frequently exceeded 100 parasites per nest. For this reason we became interested in what effects *Protocalliphora* larvae have on the survivorship of their hosts.

Apparently, larvae of all *Protocalliphora* spp. feed solely on blood of birds. Because purely hematophagous diets are deficient in the vitamin B complex (Fraenkel 1952) the diet may be supplemented by the action of gut symbiotes or from other food sources, such as yeast, in the nest (K. S. Hagen, pers. comm.). With the exception of *Protocalliphora hirudo*, which lives subcutaneously, the larvae of all Nearctic species are intermittent ectoparasites living largely in the nest material (Zumpt 1965, Bédard and McNeil 1979). *Protocalliphora hirudo* is known to remain briefly on birds after fledging (Zumpt 1965). *Protocalliphora* is the only North American genus of Diptera with hematophagous larvae (Zumpt 1965).

Opinions in the literature regarding the effects of *Protocalliphora* on nestling birds are mixed and in most instances inconclusive. Nestling mortality attributed to *Protocalliphora* has been widely reported. Early reports have been summarized by Bennett (1957). However, direct evidence demonstrating that *Protocalliphora* was, in fact, the cause of death was not provided in any of these studies. It appears that in most cases the parasite simply provided the most convenient explanation to account for nestling mortality.

Observations by others indicated that little or no nestling mortality was found in infested nests even when *Protocalliphora* numbers ranged into the hundreds per nest (Rothschild and Clay 1952). Bennett (1957) studied
2519 nests and found nestling mortality to be slight, and similar between infested and uninfested nests. Whitworth (1976) examined 1819 nests, and although finding greater nestling mortality than Bennett, concluded that Protocalliphora was only one of several stresses encountered by birds and was not directly responsible for these deaths. Eschuis-van der Voet and Kluyster (1971) noted in a progress report a relationship between timing and intensity of Protocalliphora infestation and first year survival of Great Tits (Parus major); unfortunately this study was never published.

In our study, previously established nestbox plots provided a substantial number of accessible nests to investigate the biology of Protocalliphora spp. parasitizing Mountain and Chestnut-backed chickadees. In this paper we will examine the relationship between intensity of Protocalliphora infestations and chickadee fledging rates. In this respect we were interested in seeing if there might be some threshold value of Protocalliphora numbers above which chickadee nestlings would succumb. Finally, we hypothesized that chickadees fledging from heavily infested nests would do so in a weakened condition. Since chickadees will fledge prematurely if disturbed during the latter part of the nestling period and because it was logistically impossible to follow fledglings, we attempt to look at this question through the more indirect means of relating larval biomasses to weakening of birds through prefledging blood loss.

STUDY AREAS AND METHODS

Three nestbox plots were established in 1966 in Modoc National Forest, Modoc Co., California. This forest is mixed conifer stands dominated by ponderosa pine (Pinus ponderosa) and white fir (Abies concolor) with a lesser amount of incense cedar (Calocedrus decurrens) also present. The elevation of the study sites ranged from 1625–1900 m. Each plot was formed by the placement of boxes in a grid pattern with 10 east-west parallel rows of five boxes each. All boxes were placed on trees at breast height (1.5 m) and spaced at intervals of 100 m. Prior to the 1976 breeding season additional boxes were placed in half of one plot by reducing the distance between boxes to 50 m. The nestboxes used in this study were constructed of cement and sawdust and were purchased from Schwegler and Sons of Munich, Germany. The entrance hole was 3.3 cm, the interior depth beneath the hole was 12 cm, and the inside diameter was 11 cm.

In 1972 three more nestbox plots were set up in an identical manner at Blodgett Forest Research Station, 19.5 km east of Georgetown, El Dorado Co., California. Blodgett Forest (elev. 1250–1400 m) is 1215 ha of second growth mixed conifer stands. Major tree species present are ponderosa pine, sugar pine (Pinus lambertiana), white fir, incense cedar, black oak (Quercus kelloggii), and tan oak (Lithocarpus densiflora).

In February 1978, 100 boxes were placed on East Bay municipal land, in Contra Costa County, California, situated immediately east of Tilden Park. Boxes were placed a minimum of 50 m apart without regard to pattern. Forty-nine of these boxes were placed in even-aged plantations of Monterey pine (Pinus radiata) essentially pure in character, although some California bay (Umbellularia californica) was present. The remaining 51 boxes were placed in stands of California live oak (Quercus agrifolia) with lesser amounts of California bay, interior live oak (Q. wislizenii), and big leaf maple (Acer macrophyllum). Prior to 1979, 16 of
these latter boxes were removed from an area of no nesting to replace old boxes in Modoc County and Blodgett Forest.

Active nests were checked at least once every three days. Bird nesting data included number of nestlings, fledging success, and notations on any unusual appearance in the health of the birds. The fledging period of Mountain and Chestnut-backed chickadees is 21 days; after the nestlings were 15 days old, only their presence or absence was noted to avoid premature fledging. Nestling mortality after this period was assessed by examining fledged nests for dead birds.

Most nests were collected within 3 weeks after fledging and placed in emergence containers. The number of emerging flies and their hymenopterous parasitoids were then counted. After emergence was completed puparia were counted. Because of difficulty in locating all puparia, the number of emerged puparia counted was usually less than the number of reared flies. In some cases it was greater, indicating that some flies had emerged prior to nest collection. Thus, for establishment of infestation number in a nest, the larger number was used and added to the number of unemerged puparia.

A series of nest substitutions was made by taking uninested nests collected from the Contra Costa County nestbox plots, cleaning them of arthropods in Berlese funnels, and then exchanging them for active nests in the Blodgett County and Modoc County nestbox plots. The active box was removed from the tree and replaced by a box containing the clean nest. The nestlings were then examined for Protocalliphora and transferred to this new nest. This process allowed for the determination of oviposition times and provided Protocalliphora larvae for assessment of biomass. The larvae were held for 48 h prior to weighing to allow for assimilation or voiding of gut contents.

RESULTS

Dahlsten and Copper (1979) have summarized the breeding data collected over a 10-year span for the Mountain Chickadee on the Modoc County nestbox plots and have gathered similar data for both species of chickadee for Blodgett Forest plots (Dahlsten and Copper, unpubl.). Mean annual fledging success for Mountain Chickadees in Modoc County study plots was 70.2%. This figure was obtained by dividing the total number of birds fledging by the number of eggs in completed clutches (e.g., where incubation had begun). In addition, since breeding chickadees in our study sites show strong nest-site fidelity from year-to-year, we have been able to use banding returns to estimate a first year mortality of 85% for fledglings. This figure is not unusually high for a small passerine (Welty 1962). It is believed that much of the high first year mortality in passerines occurs within the first few weeks after fledging (Lack 1966).

The Contra Costa County nestboxes were visited every 3 days in 1978, but only once a month in 1979. The late date at which the nestbox plot was established may have reduced box usage the first year as the first Chestnut-backed Chickadee egg was laid within 3 weeks of this time. In 1978 there were 19 Chestnut-backed Chickadee nesting efforts reaching the nestling stage while in 1979 there were 29. An additional seven chick-
Chickadee nests were available during these 2 years from boxes in nearby Albany and Orinda, California. With the exception of one case of vandalism, fledging occurred from all of these nests; there were no instances of predation. In 1978 all chickadee nests were free of Protocalliphora; however, a Bewick's Wren (Thryomanes bewickii) nest in one of the boxes contained 50 Protocalliphora puparia. The following year one chickadee nest was found to be infested with Protocalliphora. This nest contained 104 puparia although for an unknown reason only 12 flies emerged.

In 1977 clutches in 25 nests hatched at Blodgett Forest, of which 20 successfully fledged. Three of the successful nests were of Chestnut-backed Chickadees and the remainder were of Mountain Chickadees. Protocalliphora data were taken for 19 of the successful nests and for two that failed prematurely due to nestling mortality. In 1978 11 successful Mountain Chickadee as well as two successful and one predated Chestnut-backed Chickadee nests taken from the nestbox plots were examined for Protocalliphora. An additional Chestnut-backed Chickadee nest taken from a snag near one nestbox plot was also collected. Finally, in 1979 an additional nine Mountain and two Chestnut-backed chickadee nests were collected. Young had fledged from all of these nests.

All of the chickadee nests from Blodgett Forest were infested during these 3 years with the exception of one Chestnut-backed Chickadee nest in 1977 and one Mountain Chickadee nest in 1978 (Table 1). In the latter case, larvae had been observed in the nest, but apparently none survived to the pupal stage. Considerable variation was found in the numbers of Protocalliphora per nest (Table 1), but there were no significant differences found between the species of the chickadees (Table 1).

In 1977, 97 Mountain Chickadee nests reached the nestling stage on the Modoc County study plots. Of these, nestlings fledged from 65 nests, and 32 terminated with the death of the nestlings. Predation by weasels (Mustela spp.) and snakes was responsible for most of the mortality in these instances although the cause of clutch failure in a few nests could not be determined. Forty-seven of the fledged nests and 26 of the unsuccessful ones were examined for Protocalliphora numbers.

In 1978, 80 nests reached the nestling stage and young were fledged from 77 of these. Weasel predation occurred in one nest when the young were 17 days old and in two others when the nestlings were about 15 days old.

Infestation numbers for successful nests during both years are summarized in Table 2. As in Blodgett Forest, nearly all nests were infested. Infestation numbers in nests terminated by predation or other nestling mortality during the first 2 weeks were extremely low; over 80% of these
### Table 1

**NUMBER OF PROTOCALLIPHORA INFESTING NESTS OF CHESTNUT-BACKED AND MOUNTAIN CHICKADEES AT BLODGETT FOREST, 1977–1979**

(a) *Proto calliphora* in nest

<table>
<thead>
<tr>
<th>No. nests</th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>1–19</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>20–39</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>40–59</td>
<td>4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>60–79</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>80–99</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>100+</td>
<td>4</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Total nests</td>
<td>19</td>
<td>14</td>
<td>11</td>
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</tbody>
</table>

(b)  

<table>
<thead>
<tr>
<th></th>
<th>CBC</th>
<th>MC</th>
<th>Total</th>
<th>CBC</th>
<th>MC</th>
<th>Total</th>
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<tbody>
<tr>
<td>Nests</td>
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<td>16</td>
<td>19</td>
<td>3</td>
<td>11</td>
<td>14</td>
<td>2</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>Range</td>
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<td>0–17</td>
<td>0–273</td>
<td>112–144</td>
<td>0–173</td>
<td>0–173</td>
<td>22–133</td>
<td>20–238</td>
<td>20–238</td>
</tr>
<tr>
<td>Total larvae</td>
<td>358</td>
<td>822</td>
<td>1180</td>
<td>398</td>
<td>562</td>
<td>951</td>
<td>155</td>
<td>1042</td>
<td>1197</td>
</tr>
<tr>
<td>$\bar{x} \pm SD^c$</td>
<td>119.3±</td>
<td>51.4±</td>
<td>62.1±</td>
<td>129.7±</td>
<td>51.1±</td>
<td>67.9±</td>
<td>77.5±</td>
<td>115.8±</td>
<td>108.8±</td>
</tr>
<tr>
<td></td>
<td>133.2</td>
<td>50.4</td>
<td>68.8</td>
<td>16.3</td>
<td>54.2</td>
<td>58.5</td>
<td>78.5</td>
<td>64.8</td>
<td>67.9</td>
</tr>
</tbody>
</table>

* Chestnut-backed Chickadee.

* Mountain Chickadee.

* Differences between bird species not significant (2 sample t-tests, $P > 0.05$).
nests had fewer than 20 Protocalliphora. Thus, early host mortality led to a decrease in fly numbers, undoubtedly reducing the time available for oviposition as well as providing an insufficient period for larval development.

A series of over 250 adult Protocalliphora with their associated puparia and larvae were used for species determinations. These included material from both Chestnut-backed and Mountain chickadee nests and from all three study areas. With two exceptions, all Protocalliphora collected in or reared from chickadee nests belonged to a single new species (termed here Protocalliphora n.sp. no. 1). This species had previously been collected by Dahlsten at these study areas and in Inyo County, California. While he observed larvae each year since the study began, positive determinations were made only on material collected during the 1969 breeding season. This species was identified from nests of both species of chickadee as well as from that of a Red-breasted Nuthatch (Sitta canadensis) (Sabrosky, pers. comm.). Whitworth (1976) also collected this species in Utah, primarily from the nests of cavity nesting birds. In this study Protocalliphora n.sp. no. 1 was also reared from the nests of Brown creepers (Certhia familiaris), a Bewick's Wren, and a Barn Swallow (Hirundo rustica), but it was not found in nests of Western Bluebirds (Sialia mexicana).

### Table 2

**Infestation Numbers of Protocalliphora in Nests of Mountain chickadees at Modoc County, 1977–1978**

<table>
<thead>
<tr>
<th>(a) Protocalliphora in nest</th>
<th>No. nests</th>
<th>1977</th>
<th>1978</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>1–19</td>
<td></td>
<td>26</td>
<td>29</td>
</tr>
<tr>
<td>20–39</td>
<td></td>
<td>8</td>
<td>20</td>
</tr>
<tr>
<td>40–59</td>
<td></td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>60–79</td>
<td></td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>80–99</td>
<td></td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>100+</td>
<td></td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Total nests</td>
<td></td>
<td>47</td>
<td>80</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b)</th>
<th>1977</th>
<th>1978</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nests</td>
<td>47</td>
<td>80</td>
</tr>
<tr>
<td>Range</td>
<td>0–162</td>
<td>0–164</td>
</tr>
<tr>
<td>Total larvae</td>
<td>1093</td>
<td>2977</td>
</tr>
<tr>
<td>$\bar{x} \pm SD$</td>
<td>23.3 ± 31.3</td>
<td>37.2 ± 39.0</td>
</tr>
</tbody>
</table>

*a* Includes three nests in which entire clutch was predated after attaining age of 15 days.
Table 3

Mortality in Nests of Chestnut-backed and Mountain chickadees Fledging Young, Blodgett Forest, California, 1977–1978

<table>
<thead>
<tr>
<th>Study site and year</th>
<th>Nests examined</th>
<th>Number of nests hatched</th>
<th>Percent fledging*</th>
<th>Estimated blood loss per nestling to Protocalliphora (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blodgett 1977</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>With bird mortality</td>
<td>4</td>
<td>22</td>
<td>5</td>
<td>3.5</td>
</tr>
<tr>
<td>Most heavily infested</td>
<td>7</td>
<td>50</td>
<td>0</td>
<td>17.8</td>
</tr>
<tr>
<td>All successful nests</td>
<td>19</td>
<td>120</td>
<td>100a</td>
<td>9.8</td>
</tr>
<tr>
<td>Blodgett 1978</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>With bird mortality</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>11.1</td>
</tr>
<tr>
<td>Most heavily infested</td>
<td>5</td>
<td>35</td>
<td>0</td>
<td>18.8</td>
</tr>
<tr>
<td>All successful nests</td>
<td>6</td>
<td>93</td>
<td>99a</td>
<td>10.8</td>
</tr>
</tbody>
</table>

* For year and site, pairs with different letters are statistically significant (1-sample t-test; P > 0.05).
* Blood loss estimated at 0.125 g/larvae assuming average biomass per larvae as 0.05 g and conversion efficiency of blood to parasite biomass at 40%.
* Nests in which mortality occurred, but at least one nestling fledged.
* Nests fledging at least one young.

located within 10 m of infested chickadee nests. Instead, the bluebirds were hosts to P. sialis. Similar findings were also made by Whitworth (1976).

The exceptions included one individual of P. hirudo which was reared from the nest of a Mountain Chickadee at Blodgett Forest in 1978. This is likely an aberrant occurrence as this species normally attacks cup nesters (Bennett 1957). The second exception was a second new species of Protocalliphora which was also reared from a Mountain Chickadee nest at Blodgett Forest in 1979. At present we do not know if this species has been collected previously.

Protocalliphora n.sp. no. 1 is univoltine (producing but one generation each year) and perhaps for this reason infestation numbers did not increase as the nesting season progressed and nesting density declined. Oviposition by the flies occurs in the nest throughout the nestling stage but not before the first birds hatch. There are three larval instars, of which the first two are brief. The larvae are intermittent feeders and spend most of the time in or under the nest. Larval development may be completed before the nestlings fledge. Mature larvae enter a nonfeeding pre-pupal stage which lasts about 2 days. The pupation site is within the nest material. Details of the biology of Protocalliphora n.sp. no. 1 will be published elsewhere (Gold and Dahlsten, in press).
Table 4
Mortality in Those Nests of Mountain Chickadees Fledging Young, Modoc County, California, 1977–1978

<table>
<thead>
<tr>
<th>Study site and year</th>
<th>Nests examined</th>
<th>Number of nests</th>
<th>Nestlings hatched</th>
<th>Dead</th>
<th>Percent fledging</th>
<th>Estimated blood loss per Protocalliphora per nestling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Protocalliphora (g)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modoc</td>
<td>With bird mortality&lt;sup&gt;c&lt;/sup&gt;</td>
<td>12</td>
<td>78</td>
<td>19</td>
<td>76</td>
<td>6.5</td>
</tr>
<tr>
<td>1977</td>
<td>Most heavily infested</td>
<td>7</td>
<td>45</td>
<td>4</td>
<td>91a</td>
<td>12.7</td>
</tr>
<tr>
<td></td>
<td>All successful nests&lt;sup&gt;d&lt;/sup&gt;</td>
<td>47</td>
<td>280</td>
<td>19</td>
<td>93a</td>
<td>3.9</td>
</tr>
<tr>
<td>Modoc</td>
<td>With bird mortality</td>
<td>9</td>
<td>62</td>
<td>10</td>
<td>84</td>
<td>9.2</td>
</tr>
<tr>
<td>1978</td>
<td>Most heavily infested</td>
<td>15</td>
<td>111</td>
<td>8</td>
<td>93a</td>
<td>14.5</td>
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<tr>
<td></td>
<td>All successful nests</td>
<td>80</td>
<td>488</td>
<td>10</td>
<td>98b</td>
<td>6.1</td>
</tr>
</tbody>
</table>

* For year and site, pairs with different letters are statistically significant (1-sample t-test: t = 5.96, df = 93, P < 0.01).
* Blood loss estimated at 0.125 g/larvae assuming average biomass per larva as 0.05 g and conversion efficiency of blood to parasite biomass at 40%.
* Nests in which mortality occurred but at least one nestling fledged.
* Nests fledging at least one young.

Difficulties in working with cavity nests and the handling of older nestlings made direct measurements of parasite feeding effects untenable. Observations of the larvae feeding on the birds were uncommon and this feeding was easily disturbed. It is possible that most feeding occurred at night when the nestlings would be inactive. As an indirect means of assessing stress on nestlings, Protocalliphora larval biomasses were obtained to give a measure of parasite load. Weights of immature Protocalliphora were found to vary moderately. These weights were related to age and affected by gut contents. Maximal larval weights occasionally exceeded 100 mg and the average for third instar larvae was about 80 mg (N = 170). Prepupae averaged about 65 mg (N = 20) and the puparia weights ranged from 40–50 mg (N = 40).

DISCUSSION

Nestling mortality was slight after exclusion of that which could be attributed to predation. Occasionally all nestlings died due to unexplained causes which could include abandonment or death of parent or, conceivably, Protocalliphora feeding. However, nests in which all nestlings died before attaining 15 days of age were excluded from analysis because low parasite numbers in these nests could be attributable to the abbreviated period of host availability. In the remaining nests at Blodgett, 96.3% (N =
120) and 98.9% (N = 93) (Table 3) of these nestlings fledged in 1977 and 1978, respectively, while for Modoc County the corresponding figures were 93.2% (N = 280) and 97.9% (N = 488) (Table 4).

One-sample t-tests were performed to compare mortality in the most heavily infested nests with that in all nests from which at least one nestling fledged. Differences were not statistically significant at Blodgett Forest in 1977 and 1978 and in Modoc County in 1977. A statistically significant difference was found in Modoc County in 1978 (Table 4). Nests with mortality that year had an average infestation of 9.2 Protocalliphora per nestling. This is about 50% higher than overall average infestation of Modoc County but lower than that found at Blodgett each year.

Thus, high infestations may occasionally contribute to nestling mortality. However, the fact that no significant differences in nestling mortality were found between those heavily infested and all nests at Blodgett both years and in Modoc County in 1977 and that 93% of young in heavily infested Modoc nests fledged in 1978 suggest mortality attributable to Protocalliphora is slight. As noted, Protocalliphora numbers were low in nests where the entire clutch died before fledging indicating that it would be maladaptive for the parasites to kill their hosts. Further evidence of coevolution is suggested by the limited host range of many Protocalliphora spp. In our study we collected gravid females of several species of Protocalliphora in and around active chickadee nests but these species were never reared.

Although not evaluated in this study, post-fledging mortality may be due to the indirect effects of Protocalliphora infestations in the nest. Kluyver (Eschuis-van der Voet and Kluyver 1971) found reduced survival of Great Tits which fledged from nests heavily infested by P. azurea. Kluyver was working in isolated stands that reduced fledgling dispersal. In the Blodgett Forest and Modoc County plots, areas of vast contiguous forest, fledglings tend to disperse from the nest box plots and banding returns of these birds is 0.3% (Dahlsten and Copper 1979).

Eschuis-van der Voet (1972) and Eschuis-van der Voet and de Reede (1974) provided progress reports on their work which included a study on the effects of P. azurea on Great Tits. They noted a relationship between larval size and adverse effects on nestlings. These authors speculated that negative effects were most intense when the timing of oviposition resulted in the presence of large larvae when nestlings were near fledging. This supposition was based on evidence that Protocalliphora produced anemic conditions in nesting birds but that recovery could be rapid upon cessation of feeding by the parasites. However, fledglings in anemic condition would be less able to cope with post-fledging stresses. Whitworth (1976) also found rapid recovery could occur in nestlings unless hematocrit and hemoglobin levels fell below certain minima.
The bird work in Blodgett Forest and Modoc County was done entirely in the field. Blood analysis was deemed inappropriate because handling of nestlings after they reach an age of 14 days could cause premature fledging, and the critical period for assessing blood loss would be just prior to normal fledging. However, insight into the effects of Protocalliphora was gained by comparing biomass of parasites in a nest with that of their hosts.

Little work has been done on the blood volume, rate of hemopoeisis (especially under stress), and tolerance of blood loss in wild adult birds and less is known about nestlings. Several assumptions were employed to assess the degree of stress on nestling chickadees by Protocalliphora feeding. Mountain Chickadee adults weigh approximately 11 g (Dahlsten and Copper 1979), while adult Chestnut-backed Chickadees weigh about 10 g (Dahlsten, unpubl.). Growth rates of Mountain and Chestnut-backed chickadees are unknown, although they are comparable in size to Black-capped Chickadees (Parus atricapillus) for which daily weights during the nestling period are known (Kluyver 1961). By comparison with Kluyver’s data, the average daily weight of a Mountain Chickadee would be 8.04 g. The blood volume in a bird is about 6% of body weight (J. Kaneko, pers. comm.), thus giving an average daily blood volume of 0.48 g.

To assess the amount of blood loss, the biomass of Protocalliphora must be converted to blood consumption. Johnson (1960) found that the immature stages of the bed bug Cimex lectularius had a conversion efficiency of ingested blood to biomass of 30–40%. Similar figures are not available for hematophagous Diptera, but K. S. Hagen (pers. comm.) considered 40% to be a reasonable and conservatively high figure (in terms of host impact). Using a biomass of 50 mg as an average biomass for larvae, each would therefore have consumed an average of 0.125 g of blood during the entire larval period. From this figure blood loss to Protocalliphora can be estimated (Tables 3, 4). The range was from 0.49 g per nestling in Modoc County in 1977 to 1.35 g per nestling in Blodgett Forest in 1978. The extreme case was a nest of Chestnut-backed Chickadees in Blodgett Forest which averaged 45.5 Protocalliphora per nestling. If each larva attained average size, the mean blood loss would have been 5.69 g per nestling.

Actual blood loss suffered by nestlings may fluctuate during the nestling period. The timing and synchrony of infestations varied although there was a tendency for larval numbers and sizes to be greater during the latter stages of the nestling period; this is the period considered by Eschuis-van der Voet and de Reede (1974) and Whitworth (1976) to be the most critical.

Kaneko (pers. comm.) believed that blood loss over 25% of daily volume should be fatal and that losses of 10% or more would have negative effects on the health and development of the bird. If the average daily blood
volume is 0.48 g, then average daily blood losses of 10 and 25% summed over the 21-day nestling period would mean total losses of 1.01 and 2.52 g of blood, respectively. This would mean that parasite loads exceeding eight Protocalliphora per nestling would have debilitating effects while loads exceeding 20 larvae per nestling would be severe enough to be fatal through blood loss. However, no mortality attributable to infestations occurred in the field, even though parasite loads often exceeded the above values. In the most heavily infested nest, blood loss was probably over 55% of the total blood volume. Similarly, Bennett (pers. comm.) reported biomasses of Protocalliphora two to three times that of their Barn Swallow hosts, yet no mortality was found in these nests. Since Protocalliphora larvae are, at present, known to be solely hematophagous, it is difficult to see how these nestlings survived.

While the assumptions here are speculative, it seems clear that nestlings in heavily infested nests are suffering a tremendous loss of blood. The ability of parent birds to counteract this drain on the nestlings’ energy reserves is not known. To some extent, partial recovery may occur with the cessation of parasite feeding (Whitworth 1976) and the continued provision of food by the parents after fledging (Ricklefs 1974). However, nestling development is not uniform; consequently, stresses at specific times may lead to retardation of organs or tissues without the possibility for complete compensation even if the stress is later alleviated (O’Connor 1977). First year mortality of Mountain Chickadees has been calculated at 85% (Dahlsen and Copper 1979) and it is likely that much of this mortality occurs shortly after fledging as young inexperienced birds are confronted with many new stresses. These stresses might be aggravated in birds weakened by Protocalliphora and fledging in a somewhat anemic condition. Additionally, post-fledging success has been positively related to body size in a related species, Parus major (Perrins 1965, Garnett 1981). If blood loss from Protocalliphora feeding does, in fact, retard nestling growth, heavily attacked birds will be further disadvantaged upon fledging and still more likely to succumb.

**SUMMARY**

More than 90% of Mountain (Parus gambeli) and Chestnut-backed (P. rufescens) chickadee nests in two interior California mixed conifer habitats were found to be infested with Protocalliphora parasites. In contrast, only 1 of 55 chickadee nests was infested in a coastal study area. Failure of most puparia in this nest to develop may reflect the presence of some environmental factor unsuitable for Protocalliphora. Infestation numbers varied considerably, and in one instance the hosts fledged despite an infestation exceeding 45 Protocalliphora per nestling. Nestling mortality was low and did not seem to be related to effects of the parasites. This observed result was surprising in light of expected effects predicted from
parasite biomasses supported by many nestlings. However, fledglings stressed by blood losses resulting from heavy Protocalliphora infestations are nonetheless thought to have reduced post-fledging success.

ACKNOWLEDGMENTS

We are especially grateful for field assistance from K. Sheehan, W. Copper and A. P. Gutierrez. We wish to thank C. Sabrosky of the U.S. National Museum and G. F. Bennett of the International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland, for identifications and suggestions. We are also thankful to J. R. Anderson and K. S. Hagen (Department of Entomology) and R. Barrett (Department of Wildlife and Fisheries) of the University of California, Berkeley, for their helpful advice during this study. J. J. Kaneko of the Department of Clinical Pathology, University of California, Davis, provided information on blood production in nestling birds. Finally, we wish to thank R. Barrett, S. F. Bailey (Museum of Vertebrate Zoology, University of California, Berkeley), and K. L. Dixon (Department of Biology, Utah State University) for their comments and critical review of the manuscript. These studies were funded in part by the USDA, Secretary of Agriculture, Douglas Fir Tussock Moth R&D Program.

LITERATURE CITED


DIV. BIOLOGICAL CONTROL, UNIV. CALIFORNIA, BERKELEY, 1050 SAN PABLO AVE., ALBANY, CALIFORNIA 94706. ACCEPTED 15 APR. 1983.

The Wilson Ornithological Society will hold its 1984 Annual Meeting at the University of North Carolina, Wilmington, in conjunction with the Annual Meeting of the Carolina Bird Club, 31 May–3 June. JAMES F. PARNELL, Biology Department, University of North Carolina, Wilmington, NC 28401, is chairing the local committee. MARY H. CLENCH, 2239 NW 21st Ave., Gainsville, FL 32605, will guide the scientific program.
SITE-RELATED NESTING SUCCESS OF MOURNING DOVES AND AMERICAN ROBINS IN SHELTERBELTS

RICHARD H. YAHNER

Farmstead shelterbelts are often the only source of wooded habitat amid extensive croplands and pastures in the intensively-farmed regions of the Midwest (Griffith 1976), thereby representing an important habitat for many species of birds (Martin 1980; Yahner 1982a, 1983a). Mourning Doves (Zenaida macroura) and American Robins (Turdus migratorius) are among the most abundant nesting species of birds in Minnesota farmstead shelterbelts (Harris et al. 1963, Yahner 1982b). In a previous study of nest-site selection by five avian species in shelterbelts based on total nests constructed (active and inactive nests pooled), I found considerable overlap between doves and robins in both choice of nesting substratum and microhabitat features surrounding nest-sites (Yahner 1982b).

Selection should ensure that individuals that construct nests in optimal microhabitat locations are more successful in fledging young than individuals that choose less suitable locations (Caccamise 1977). In shelterbelts, nesting success has been reported for doves (e.g., Boldt and Hendrickson 1952, Randall 1955, Harris et al. 1963) but not for robins. Further, nesting success of both species in relation to microhabitat features or nesting substrata has seldom been examined (but see Howell 1942, Coon et al. 1981). Because of pronounced similarities in nest-site selection between doves and robins in shelterbelts (Yahner 1982b), herein I specifically examine whether or not success of active nests is associated with microhabitat features or other site-related factors either within a species or between the two species. Two hypotheses are tested: (1) microhabitat features of active nest-sites do not vary among successful and unsuccessful nests of doves and robins; and (2) relative densities of potential predators among shelterbelts do not affect nesting success in these two avian species.

STUDY AREA AND METHODS

The study was conducted at the Rosemount Agricultural Experiment Station, Dakota Co., Minnesota, from June 1978–July 1981. Topography at the Station is flat to gently rolling; agricultural practices and land uses are characteristic of intensively-farmed regions of southern Minnesota (Yahner 1982a). Seven representative farmstead shelterbelts were selected for study (details of each are presented in Yahner 1980a, 1982b).

Nest searches were made every 2–3 days when possible from March to late September in each shelterbelt by systematically searching the ground level and all trees and shrubs for active nests of Mourning Doves and American Robins. Active nests were defined as containing one or more eggs or nestlings (Harris et al. 1963) in newly-constructed nests, in
abandoned nests of conspecifics, or in abandoned nests constructed by another species. Inactive nests (see Yahner 1982b) were not included in this study. An effort was made to monitor the status of each active nest every 1–3 days. Successful active nests were those in which one young was fledged or known to be present in the nest within 1 day of the expected date of fledging, in cases where individual active nests could not be inspected on the exact day of fledging (see Coon et al. 1981).

Six microhabitat features were measured for each active nest: (1) compass direction of the nest relative to the position of the main stem of the tree or shrub containing the nest; (2) height (m) of the tree or shrub in which the active nest was located; (3) height (m) of the nest above ground; (4) diameter (m) of the largest woody stem touching and/or supporting the nest; (5) lateral distance (m) of the nest from the main trunk of the tree or shrub containing the nest; and (6) species of tree or shrub used as nesting substratum.

Active nests of doves and robins were divided into successful and unsuccessful nests, giving four groups of active nests for statistical analysis. Rates of nesting success were compared between bird species using tests of equality between two percentages based on arcsine transformations (statistical tests throughout are from Sokal and Rohlf 1969). Compass direction among the groups of nests was analyzed by categorizing an active nest as being north (315–45°), east (45–135°), south (135–225°), or west (225–315°) of the main stem of the nesting substratum; the resultant 4 × 4 data matrix was analyzed by a row (R) × column (C) test of independence. Differences in means of nesting substratum height, nest height, nesting substratum diameter, and nest distance to main trunk of nesting substratum among the four groups of active nests were examined by single-classification analyses of variance and Student-Newman-Keuls tests. If necessary, data were transformed with square roots prior to analysis. To determine relationships between nesting success of both avian species and nesting substrata used, active nests occurring in major genera of trees and shrubs (genera containing at least 10% of the total nests) were analyzed via a R × C test of independence. Rows of the data matrix were spruce (Picea spp.), maple (Acer spp.), and ash (Fraxinus spp.), and columns were the four groups of active nests.

The potential effect of mammalian predators on nesting success was determined by first dividing shelterbelts into those containing resident populations of predators vs those with no or transient populations of predators. Two potential mammalian predators regularly observed and/or live-trapped at the Station and known to prey on the contents of bird nests (Nelson 1976, Gates and Gysel 1978) were red squirrels (Tamiasciurus hudsonicus) and house cats (Felis domesticus) (Yahner 1980b, 1983b). Active nests in the four groups (rows) of active nests were analyzed between the two categories of shelterbelts (columns) using a R × C test of independence for each predator separately. Potential avian predators, such as Blue Jays (Cyanocitta cristata) or Common Grackles (Quiscalus quiscula) (McClure 1943, Harris et al. 1963, Best 1978), were not considered because both species nested and/or regularly visited all seven shelterbelts during the study (Yahner 1983a).

RESULTS AND DISCUSSION

Reuse of nests.—Ninety-four and 54 active nests of Mourning Doves and American Robins, respectively, were monitored during the study. Robins nested only in newly-constructed nests and never in abandoned nests. Robins seldom reuse nests of either conspecifics or other species (Howell 1942). However, only 70 (75%) active nests of doves were newly-constructed dove nests; 13 (14%) were in abandoned dove nests, 7 (7%) in abandoned grackle nests, and 4 (4%) in abandoned robin nests. Other studies
Table 1

<table>
<thead>
<tr>
<th>Nest group</th>
<th>Total active nests</th>
<th>North (315-45°)</th>
<th>East (45-135°)</th>
<th>South (135-225°)</th>
<th>West (225-315°)</th>
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<tbody>
<tr>
<td>Successful dove nest</td>
<td>30</td>
<td>3</td>
<td>9</td>
<td>12</td>
<td>6</td>
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<tr>
<td>Unsuccessful dove nest</td>
<td>64</td>
<td>7</td>
<td>17</td>
<td>31</td>
<td>9</td>
</tr>
<tr>
<td>Successful robin nest</td>
<td>30</td>
<td>4</td>
<td>10</td>
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<tr>
<td>Unsuccessful robin nest</td>
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</tbody>
</table>

have shown that doves are very opportunistic in using abandoned nests (e.g., McClure 1946, Boldt and Hendrickson 1952, Harris et al. 1963) and artificial nests (Nelson 1976). Greater use by doves of abandoned grackle nests vs abandoned robin nests in my study was not unexpected due to the greater number of available grackle nests in the seven shelterbelts. Total (active and inactive) grackle nests (N = 335) during a 2-year period (1978–1979) were nearly four times as abundant as total robin nests (N = 87); however, total dove nests (N = 136) also were less frequent than grackle nests (Yahner 1982b). This suggests that doves prefer abandoned nests of conspecifics rather than those of coexisting species. McClure (1946) observed the same dove nest being used on five different occasions during the same nesting season; I noted one dove nest to be used four times during a single season by one or more pairs of doves. I had no evidence that doves reused nests constructed in a previous year as has been noted in other studies (Coon et al. 1981).

Nesting success between species and in relation to wind damage.—Thirty active nests each of both doves (32%) and robins (56%) successfully fledged one or more young (Table 1); these rates varied between species (t = 2.8, df = 146, P < 0.01). Nesting success of doves in various habitats has ranged from about 35% in Michigan woodlots (Caldwell 1964) to 77% in a North Dakota shelterbelt devoid of predators (Randall 1955). Differential success of doves vs robins may be attributed partially to structure of nests. Doves construct “flimsy” nests compared to those of robins (Howell 1942, McClure 1943, Coon et al. 1981). But nests of both species apparently were affected equally by wind damage; seven nests (7%) of doves and two nests (4%) of robins were destroyed by high winds that accompanied severe storms (t = −1.0, df = 146, P > 0.05). Other investigators report
low dove nest loss (less than 5%) due to inclement weather (Boldt and Hendrickson 1952, Randall 1955) even though wind velocities are often excessive near shelterbelts (Lyles 1976). Summer storms in southern Minnesota usually have northerly or westerly winds, and most nests (76%) of doves in this region are located on southwest, south, east, or southeast sides of nesting substrata (Harris et al. 1963). In my study, 73% (N = 69) and 70% (N = 38) of active nests of doves and robins, respectively, were positioned east or south of the main stems of nesting substrata (Table 1). Compass direction of nest was independent of nesting success in both species (G = 4.0, df = 9, P > 0.50).

Nesting success in relation to other microhabitat characteristics.—In a previous study (Yahner 1982b), height of both nesting substratum and nest did not vary (P > 0.05) between total nests (active and inactive combined) of doves and robins during a 2-year period; whereas nesting substratum diameter was significantly less (P < 0.05) and nest distance to main trunk was significantly greater (P < 0.05) in total nests of doves compared to robins. When I compared these four microhabitat characteristics in relation to nesting success using active nests only in the present study, nest height (\( \bar{x} = 1.9-2.1 \) m) and nesting substratum diameter (\( \bar{x} = 0.05-0.07 \) m) did not differ among successful and unsuccessful nests of doves and robins (F’s < 1.4; df = 3, 144; P’s > 0.05) (Table 2). Best (1978) also noted that nest height above ground did not affect nesting success in Field Sparrows (Spizella pusilla).

Nest distance to main trunk and nesting substratum height varied among the four groups of nests (F’s > 3.2; df = 3, 144; P’s < 0.05). A posteriori comparisons of group means showed no differences (P > 0.05) between

---

**Table 2**

Mean (±SD) of Four Microhabitat Features of Successful and Unsuccessful Active Nests of Mourning Doves and American Robins in Minnesota Farmstead Shelterbelts

<table>
<thead>
<tr>
<th>Microhabitat feature</th>
<th>Nest group</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Doves</td>
<td>Robins</td>
<td>Doves</td>
<td>Robins</td>
</tr>
<tr>
<td>Height of nesting substratum (m)</td>
<td>8.0 ± 4.0*</td>
<td>6.9 ± 2.7</td>
<td>5.5 ± 3.0</td>
<td>6.6 ± 3.3</td>
<td></td>
</tr>
<tr>
<td>Height of nest (m)</td>
<td>2.1 ± 1.3</td>
<td>2.0 ± 0.8</td>
<td>1.9 ± 1.3</td>
<td>1.9 ± 1.1</td>
<td></td>
</tr>
<tr>
<td>Diameter of nesting substratum (m)</td>
<td>0.05 ± 0.06</td>
<td>0.05 ± 0.05</td>
<td>0.07 ± 0.07</td>
<td>0.06 ± 0.05</td>
<td></td>
</tr>
<tr>
<td>Nest distance to main trunk (m)</td>
<td>0.61 ± 0.69*</td>
<td>0.65 ± 0.62</td>
<td>0.29 ± 0.55</td>
<td>0.48 ± 0.46</td>
<td></td>
</tr>
</tbody>
</table>

* Significant difference (P < 0.05) in means among four nest groups, based on single-classification analysis of variance; nonsignificant ranges are underlined, based on Student-Newman-Keuls tests.
successful and unsuccessful nests of robins with respect to nest distances to main trunk ($\bar{x} = 0.29$ vs $0.43$ m) or nesting substratum height ($\bar{x} = 5.5$ vs. $6.6$ m). Likewise, successful and unsuccessful nests of doves did not vary ($P > 0.05$) with regard to nest distance to main trunk ($\bar{x} = 0.61$ vs $0.65$ m) or nesting substratum height ($\bar{x} = 8.0$ vs $6.9$ m). However, both of these characteristics were lower for successful nests of robins ($P < 0.05$) than those of either successful and unsuccessful nests of doves. Perhaps robin nests are near the main stem of a nesting substratum because their nests are bulkier than nests of doves, requiring sturdier locations to support their weight. A by-product of this selection for nest placement in robins may be greater protection from inclement weather and certain types of predators (e.g., Blue Jay), contributing to greater nesting success (56%) compared to that of doves (32%) observed in this study.

Caccamise (1977) found reduced nesting success in Red-winged Blackbirds (Agelaius phoenicus) nesting in taller shrubs and concluded that nests in tall shrubs were more susceptible to predators than nests located nearer to ground level. Although nesting success of doves and robins in my study was not dependent on use of spruce, maple, or ash as nesting substrata ($G = 5.0$, df = 6, $P > 0.50$), both species nested in Picea more often than in most other plant genera in shelterbelts due to branching characteristics and regardless of tree height (Yahner 1982b). However, resident red squirrels were found in shelterbelts containing mature spruce that produced large quantities of cone seeds as a food source (Yahner 1980b). I suggest that possibly small Picea were used less often by foraging squirrels (Sciuridae), accounting in part for the relationship between successful robin nests and low height of nesting substrata.

Nesting success in relation to predators.—Of 64 and 24 unsuccessful nests of doves and robins (Table 1), respectively, similar ($t = -0.05$, df = 86, $P > 0.05$) proportions of these unsuccessful dove (80%) and robin nests (79%) were lost to predation. Relative densities of house cats in farmsteads adjacent to shelterbelts were independent of nesting success of both avian species ($G = 1.4$, df = 3, $P > 0.05$). Several studies in rural areas have found little predation by house cats on birds (e.g., Parmalee 1953). In contrast, relative densities of red squirrels in shelterbelts were dependent on nesting success ($G = 9.2$, df = 3, $P < 0.05$). Proportions of successful dove nests did not differ between shelterbelts inhabited by resident red squirrels (38%) and shelterbelts lacking resident squirrels (37%). However, only 40% of total active robin nests were successful in shelterbelts occupied by red squirrels compared to 67% success rate for nests in shelterbelts infrequently used by this mammal. These differential success rates may imply a greater nest predation on...
robins than on doves by *Tamiasciurus*. I propose that behavior associated with parental defense of nests by robins (e.g., attack; see Howell 1942) may increase the conspicuousness of a concealed robin nest (e.g., a nest close to the tree trunk) to arboreal red squirrels rather than acting as an effective deterrent against predation.

Nesting success in relation to season.—Nests were initiated from April–August by doves and from April–June by robins. Percentages of successful nests per month in doves ranged from 30% in June (N = 23 active nests) to 50% in August (N = 2). Success rates of 32% in April (N = 19), 33% in May (N = 39), and 36% in July (N = 11) were similar in doves giving no consistent trend in monthly success rates. LaPointe (1958) observed no seasonal trend in nesting success of doves, whereas Harris et al. (1963) and Caldwell (1964) noted greater success in latter months of the breeding season. I found that success rate of robins increased as the breeding season progressed with 50% in April (N = 26 active nests), 56% in May (N = 18), and 70% in June (N = 10). Howell (1942) also reported increased nesting success in robins with seasonal progression.

Use of coniferous vs deciduous nesting substrata by robins in my study was dependent on season (G = 32.2, df = 2, P < 0.001); 73%, 50%, and 30% of active robin nests constructed during April, May, and June, respectively, were in conifers (principally *Picea*). Of the total individual trees and shrubs present in the seven shelterbelts (N = 3589), 34% were coniferous (Yahner 1982b). As in the present study, Howell (1942) noted that robins more often nested in deciduous trees compared to coniferous trees later in the season. Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) and predation have been identified as potential factors accounting for differential nesting success in passerines over season (Best 1978), but I had no evidence that either affected nesting success.

In conclusion, two characteristics of nest-sites considered in this study were related to nesting success of robins, but none was associated with success of doves. Perhaps other characteristics of shelterbelts not measured in my study (e.g., food resources, proximal land-use features; Yahner 1983a) had important influences on nesting success. Alternatively, shelterbelts are evolutionarily-recent, man-made habitats compared to natural Midwest habitats (e.g., riparian habitats [Stauffer and Best 1980]). Although doves and robins are common nesting species in shelterbelts, they may not be adapted to these recent habitats relative to other habitats that have been in existence for longer time periods (after Gates and Gysel 1978).

SUMMARY

Nesting success of Mourning Doves (*Zenaida macroura*) and American Robins (*Turdus migratorius*) was studied for 3 years in Minnesota farmstead shelterbelts. Of 94 dove nests
and 54 robin nests, 32% and 56%, respectively, fledged at least one young. Doves frequently nested in abandoned nests, whereas robins never nested in abandoned nests. No nest-site characteristics measured in the study were related to nesting success of doves; height of tree or shrub used for nesting and distance of nest from the main stem of the nesting substratum were associated with success of robin nests when compared to those of doves. Relative to nests of doves, nests of robins may be more susceptible to predation by red squirrels. Nesting success rates of doves did not show a seasonal trend, but rates of robins increased as breeding season progressed. Farmstead shelterbelts are relatively recent, man-made habitats in the Midwest. Thus, relationships between nest-site selection and nesting success may be different than those found in habitats that have been in existence for longer time periods.

ACKNOWLEDGMENTS

I thank M. W. Weller, T. E. Martin, and R. N. Conner for helpful comments on the manuscript. This research was funded by the Minnesota Agricultural Experiment Station and by grants from the Graduate School of the University of Minnesota, The National Rifle Association of America, and The Max McGraw Wildlife Foundation. This is paper No. 13,000 of the Minnesota Agricultural Experiment Station, Scientific Journal Series, University of Minnesota, St. Paul.

LITERATURE CITED


INTERSEXUAL HABITAT PARTITIONING IN YELLOW-RUMPED WARBLERS DURING THE BREEDING SEASON

KATHLEEN E. FRANZREB

Intersexual differences in foraging behavior have been noted for a number of avian species (Selander 1966; Jackson 1970; Kilham 1970; Wilson 1970; Kisiel 1972; Grubb 1975; Williams 1975, 1980; Winkler 1979; Jenkins 1979), mainly members of the order Piciformes. Relatively limited research has been conducted on variation in foraging ecology between sexes of passerines (Morse 1967, 1968; Williamson 1971; Holmes et al. 1978).

The objective of this study was to ascertain if there were any significant differences between the foraging behavior of male and female Yellow-rumped Warblers (Dendroica coronata) during the breeding season in mixed-coniferous forest. Three possible explanations to account for any such differences are examined including: (1) habitat partitioning in order to facilitate efficient exploitation of resources by reducing intra-pair competition; (2) the influence of reproductive responsibilities (territorial advertisement and defense, location of nests, incubation duties, etc.) and its relationship to optimal foraging behavior; and (3) the hypothesis that foraging strategy merely reflects, and is strongly influenced by, what is available in the portions of the habitat actually used.

STUDY AREA

The Willow Creek watershed is located in the Apache-Sitgreaves National Forest approximately 80 km south of Springerville, Greenlee Co., in the White Mountains of Arizona. The watershed is covered by a mixed-coniferous forest and elevation ranges from 2682–2805 m.

The overall tree density was estimated at 626.2 trees per ha with Douglas-fir (Pseudotsuga menziesii) having the highest density followed by ponderosa pine (Pinus ponderosa) and southwestern white pine (Pinus strobiiformis). Douglas-fir also had the highest relative dominance and relative frequency values. For a more thorough description of the vegetation components, please see Franzreb (1978) or Franzreb and Ohmart (1978).

METHODS

Vegetation analysis.—A 15.5-ha study plot was established using a system of nine parallel, flagged transect lines 390 m in length and 50 m apart. The plotless point-quarter method was used to sample the vegetation. Tree heights of 400 mature trees were estimated using a clinometer and subsequently classified into 3-m intervals. Additional details of the vegetation analysis are available in Franzreb (1978) and Franzreb and Ohmart (1978).

Foraging behavior.—Foraging data on male and female Yellow-rumped Warblers were obtained from mid-May through August in 1973 and 1974 as I systematically traversed the transect lines. Observations were taken under skies that were generally clear to less than

581
30% overcast and wind conditions varied from no wind to light wind (Beaufort scale 0–2). Although data were collected throughout the day, the majority of observations were taken during morning hours (06:00–10:00).

Data were obtained by recording observations on an individual for as long as it was visible (frequently several minutes). For statistical purposes it is desirable to use just the first observation to reduce sampling bias. However, males are more conspicuous than females, especially during the nesting season when singing is prevalent; thus, if just the first observation is used during the analysis, the results may be biased to foraging locations near song posts. To test the effect of enhanced male detectability, I segregated the data into “first observations” and “all observations combined” and compared them using the G-test (Sokal and Rohlff 1969). There were no significant differences (P ≤ 0.05) in any of the seven foraging variables tested, hence, data reported here represent first observations.

Data were collected on seven variables related to the foraging niche of the species: method of prey procurement, perch type, perch diameter, distance from the branch tip to the perch site, tree species preferences, tree height, and bird location in the tree relative to the ground. Nine types of trees (eight species and dead trees) were identified as foraging substrates. With each observation the height of the tree in which the bird foraged was recorded using a clinometer. Also, the distance of the bird relative to the ground was estimated and denoted as “height from ground.”

The G-statistic was used to determine if statistically significant (P ≤ 0.05) differences in foraging behavior between male and female Yellow-rumped Warblers existed for the seven foraging variables. Mean tree height selection and foraging height for males and females were compared using a t-test.

Niche overlap between males and females was determined from \( O_{xy} = 1 - \frac{1}{2} \sum |P_{xi} - P_{yi}| \) (Schoener 1968) where \( P_{xi} \) is the proportion of observations of use of resource state \( i \) by males (x) and \( P_{yi} \) the use of resource state \( i \) by females (y). \( O_{xy} \) represents the extent of niche overlap between males (x) and females (y) with total overlap along a dimension yielding a value of 1. An indication of niche breadth was estimated by calculating the proportional similarity index (Feinsinger 1981) whereby \( PSI = 1 - \frac{1}{2} \sum |p_i - q_i| \). Here \( p_i \) is the proportion of resource items in state \( i \) used by male (or female) warblers and \( q_i \) is the proportion of items in state \( i \) available to the birds. The PSI was calculated separately for each sex and was only determined for those variables for which it was possible to quantify resource availability (distance from tip, tree species, tree height, foraging height).
Table 2
Perch Type Selected by Male and Female Yellow-rumped Warblers while Foraging

<table>
<thead>
<tr>
<th>Perch type</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trunk</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Branch/twig</td>
<td>381</td>
<td>189</td>
</tr>
<tr>
<td>Leaf</td>
<td>63</td>
<td>31</td>
</tr>
<tr>
<td>Total</td>
<td>446</td>
<td>220</td>
</tr>
</tbody>
</table>

Niche overlap 0.99

*No significant difference (G = 1.8, df = 3, P > 0.50).

RESULTS

Foraging behavior.—There were no significant differences between the sexes in method of prey procurement (Table 1), perch type (Table 2), diameter of the perch (Table 3), or distance from the branch tip to the foraging site (Table 4). Niche overlap for these foraging variables ranged from 0.91 to 0.99 (Tables 1–4). Niche breadth was high for distance from the tip because each sex was quite specialized in the portion of the branch selected.

Tree species selection was significantly different (G = 65.2, df = 8, P < 0.001) in that females relied heavily on Douglas-fir (34.1%) which was used by males only 18.2% of the time (Table 5). In contrast, males selected Engelmann spruce (Picea engelmannii) considerably more frequently than females (28.7% vs 19.2%). Tree species use showed the lowest degree of niche overlap (0.71) of any foraging variable (Table 5). Females were more generalized than males in this regard as demonstrated by the proportional similarity indices (0.76 female, 0.65 male) (Table 5).

The sexes differed significantly (G = 20.2, df = 3, P < 0.001) in terms of the heights of the trees used for foraging purposes (Table 6). In addition, the mean tree height used by males was significantly higher (t = 2.37, df = 647, P < 0.02) than the mean tree height for females (male $\bar{x}$ = 26.9 ± 10.1 m; female $\bar{x}$ = 24.1 ± 10.4 m), although there was considerable overlap (niche overlap = 0.85) (Table 6). Males were also decidedly more specialized than females in tree height selection (PSI = 0.37 male, 0.52 female); in fact, both sexes were more specialized in this variable than in any other foraging characteristic.

Males and females foraged at significantly different heights (G = 33.2, df = 3, P < 0.001) above the ground (Table 7). Also, female mean foraging
Table 3
Diameter of Perches Selected by Foraging Male and Female Yellow-rumped Warblers

<table>
<thead>
<tr>
<th>Perch diameter(^a)</th>
<th>No. of observations and percent</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td></td>
</tr>
<tr>
<td>&gt;5.10 cm</td>
<td>32 7.0%</td>
<td>12 6.3%</td>
<td></td>
</tr>
<tr>
<td>&gt;2.54 ≤ 5.10 cm</td>
<td>47 10.2%</td>
<td>8 4.2%</td>
<td></td>
</tr>
<tr>
<td>&gt;1.27 ≤ 2.54 cm</td>
<td>55 12.0%</td>
<td>23 12.2%</td>
<td></td>
</tr>
<tr>
<td>≤1.27 cm</td>
<td>325 70.8%</td>
<td>146 77.3%</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>459 100.0%</td>
<td>189 100.0%</td>
<td></td>
</tr>
</tbody>
</table>

Niche overlap 0.91

\(^a\) No significant difference (G = 7.4, df = 3, P > 0.05).

height was significantly lower than that of males (\(t = 2.45, df = 649, P < 0.05\)) (female \(\bar{x} = 14.7 \pm 7.1\) m; male \(\bar{x} = 17.7 \pm 7.0\) m); over 80% of female foraging observations occurred up to 18 m from the ground, whereas approximately 60% of the male foraging observations occurred within that height interval. There was substantial niche overlap (0.78) in foraging height; and females were slightly less specialized (PSI = 0.56 male, 0.61 female) (Table 7).

**DISCUSSION**

There are at least three possible explanations for the differences in foraging behavior displayed by male and female Yellow-rumped Warblers.

Table 4
Male and Female Yellow-rumped Warbler Foraging Sites with Respect to Distance from the Branch Tips

<table>
<thead>
<tr>
<th>Distance from branch tip(^a)</th>
<th>No. of observations and percent</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td></td>
</tr>
<tr>
<td>0–33% from tip</td>
<td>215 48.5%</td>
<td>93 39.1%</td>
<td></td>
</tr>
<tr>
<td>&gt;33–66% from tip</td>
<td>138 31.2%</td>
<td>87 36.5%</td>
<td></td>
</tr>
<tr>
<td>&gt;66% from tip</td>
<td>90 20.3%</td>
<td>58 24.4%</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>443 100.0%</td>
<td>238 100.0%</td>
<td></td>
</tr>
</tbody>
</table>

Niche overlap 0.91

Proportional similarity index 0.85

\(^a\) No significant difference (G = 5.6, df = 2, P > 0.10).
These are: (1) that the differences promote habitat partitioning and thus a reduction in intraspecific competition between the pair resulting in more thorough and efficient use of available resources (alternative 1); (2) that males forage closer to song posts and females forage nearer to nest-sites, thereby reducing energy expenditures and maximizing fitness (alternative

**TABLE 5**

**Tree Species Selected by Foraging Male and Female Yellow-rumped Warblers**

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine</td>
<td>128 28.7%</td>
<td>21 10.1%</td>
</tr>
<tr>
<td>Southwestern white pine</td>
<td>52 11.7%</td>
<td>24 11.6%</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>81 18.2%</td>
<td>71 34.1%</td>
</tr>
<tr>
<td>Alpine fir</td>
<td>5 1.1%</td>
<td>10 4.8%</td>
</tr>
<tr>
<td>White fir (Abies concolor)</td>
<td>21 4.7%</td>
<td>22 10.6%</td>
</tr>
<tr>
<td>Blue spruce (Picea pungens)</td>
<td>4 0.9%</td>
<td>4 1.9%</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>128 28.7%</td>
<td>40 19.2%</td>
</tr>
<tr>
<td>Quaking aspen (Populus tremuloides)</td>
<td>23 5.1%</td>
<td>16 7.7%</td>
</tr>
<tr>
<td>Snag (dead tree)</td>
<td>4 0.9%</td>
<td>0 0.0%</td>
</tr>
<tr>
<td>Total</td>
<td>446 100.0%</td>
<td>208 100.0%</td>
</tr>
</tbody>
</table>

Niche overlap 0.71

Proportional similarity index 0.65 0.76

---

*Significant difference (G = 65.2, df = 8, P < 0.001).

Based on relative density data.

**TABLE 6**

**Comparison of Tree Height Selection by Foraging Male and Female Yellow-rumped Warblers**

<table>
<thead>
<tr>
<th>Tree height* (m)</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤9 m</td>
<td>36 8.1%</td>
<td>21 10.2%</td>
</tr>
<tr>
<td>&gt;9 m ≤ 18 m</td>
<td>50 11.3%</td>
<td>50 24.3%</td>
</tr>
<tr>
<td>&gt;18 m ≤ 27 m</td>
<td>144 32.5%</td>
<td>60 29.1%</td>
</tr>
<tr>
<td>&gt;27 m</td>
<td>213 48.1%</td>
<td>75 36.4%</td>
</tr>
<tr>
<td>Total</td>
<td>443 100.0%</td>
<td>206 100.0%</td>
</tr>
</tbody>
</table>

Niche overlap 0.85

Proportional similarity index 0.37 0.52

---

*Significant difference (G = 20.2, df = 3, P < 0.001).
2); and (3) that because the sexes forage in different parts of the habitat which are probably different with respect to the abundance and distribution of prey, dissimilar foraging patterns emerge to allow the birds to forage most efficiently (alternative 3). All three alternative explanations can be tied in varying degrees to optimal foraging theory. Models dealing with this theory assume that the fitness of a foraging animal is dependent on its foraging efficiency which is usually measured in terms of net energy, and that it is selectively advantageous to forage so as to maximize fitness (Pyke et al. 1977).

In examining the merits of alternative 1, it may be argued that a reduction in intraspecific competition is largely dependent on morphological divergence. Although morphological variation is often reflected in differential foraging behavior, it is not a requisite for such differences (Ligon 1968, Jackson 1970, Kisiel 1972). Results from extensive research on woodpeckers (Picidae), including cases where sexes are morphologically similar, indicate intersexual differences in diameter of foraging perch, tree species preferences, foraging heights from the ground, and method of foraging.

In this study food may not have been limiting; hence, the high niche overlap values observed for several foraging variables should not be construed as indicative of substantial competition because there may have been no severe competition in regard to those particular variables. Schoener (1974) noted that high overlap along certain dimensions may not be relevant in appraising competition if the dimensions are not those important in partitioning the resources. Overlap indices may fail as measures of

### Table 7

<table>
<thead>
<tr>
<th>Height from ground (m)</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤9 m</td>
<td>78</td>
<td>45</td>
</tr>
<tr>
<td>&gt;9 m ≤ 18 m</td>
<td>193</td>
<td>121</td>
</tr>
<tr>
<td>&gt;18 m ≤ 27 m</td>
<td>162</td>
<td>31</td>
</tr>
<tr>
<td>&gt;27 m</td>
<td>16</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>449</td>
<td>202</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Male (0.0%)</th>
<th>Female (100.0%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niche overlap</td>
<td>0.78</td>
<td></td>
</tr>
<tr>
<td>Proportional similarity index</td>
<td>0.56</td>
<td>0.61</td>
</tr>
</tbody>
</table>

*Significant difference (G = 33.2, df = 3, P < 0.001).

Based on tree height frequency data (Franzreb, unpubl.).
of competition if the resource examined is not in short supply; in such cases even complete overlap will not result in competition (Colwell and Futuyma 1971, Hurlbert 1978). These same limitations apply to proportional similarity indices.

The first alternative indicates that warblers segregate the habitat via differences in foraging behavior to promote a reduction in competition. If this is the main reason for the variation in foraging behavior between the sexes, one might expect to see similar partitioning during the winter, assuming that food is not more abundant then than in the summer (a reasonable assumption given the primarily insectivorous diet of this species). Yellow-rumped Warblers frequently forage in intraspecific or mixed-species flocks during the winter (Wilz and Giampa 1978). The cohesive intraspecific flocks frequently formed by Yellow-rumped Warblers suggest that males and females are foraging in the same locations (similar tree heights, tree species, foraging heights, etc.) (K. J. Wilz, pers. comm.). These foraging variables are the primary distinguishing factors in habitat partitioning during the breeding season. If intersexual differences in foraging behavior were necessary to efficiently partition resources to obtain sufficient food and diminish competition, one would assume such partitioning would be evident in the winter as well as in the summer. Limited information suggests this is not the case. Hence, although the evidence is circumstantial, it would seem that intraspecific competitive influences are not the sole or primary motivating forces behind the differences observed during the breeding season in warbler foraging behavior. Alternative 1, therefore, appears to be unlikely.

Alternative 2 implies that the sexes segregate the habitat to increase foraging efficiency and maximize fitness. Net dietary food gain for energy purposes depends upon such factors as searching time, handling time, and food values (Pyke et al. 1977). In addition, other activities aside from foraging (such as time devoted to territorial advertisement and defense, escape from predators, and nesting duties), must also be considered in a bird's overall energy budget. Studying the foraging behavior of male and female spruce-woods warblers in coastal Maine, Morse (1968) noted that male Magnolia Warblers (D. magnolia), Myrtle (=Yellow-rumped) Warblers, Black-throated Green Warblers (D. virens), and Blackburnian Warblers (D. fusca) foraged nearer to the heights of their singing perches than to the heights of their nests. In contrast, the females foraged closer to their nests than to the males' singing perches. He suggested that the basic differences arose because males must be conspicuous in maintaining their territories; since a considerable amount of time is spent in that pursuit, it behooves males to forage close to the singing posts which are generally at or near the tops of the trees. On the other hand, females generally nest
considerably lower than singing perch heights. Nests of Yellow-rumped Warblers are usually constructed 1–15 m from the ground, near the ends of branches generally in conifers (Reilly 1968). Thus, it should be more energy efficient for females to forage lower in the vegetation, all other factors being equal. Less energy would then be expended in movement and hunting for prey, therefore the total caloric intake necessary for body maintenance should be at least slightly reduced, and depending on conditions, may even be substantially less.

Regarding tree height use, the preference of male warblers to select tall trees may also reflect foraging near the most conspicuous locations which are well-suited as song posts. Indeed, males not only foraged higher in the trees than females, but also selected substantially taller trees.

Tree species selection may be influenced by differences in food availability, abundance, and distribution among various locations within the vegetation profile. Males were more selective of tree species, possibly the result of their greater propensity for selecting taller trees and/or foraging higher above the ground. This may result because certain tree species generally are taller than others. The majority of male observations occurred in the three tree species which tended to be the tallest trees on the watershed (ponderosa pine, Douglas-fir, and Engelmann spruce). Tree height use and tree species selection also lend support to alternative 2 in that both appear related to reproductive duties and concomitant differences in foraging to maximize both energy intake and success in care of young. This appears to be the most persuasive alternative.

Alternative 3 implies that because sexes forage in different parts of the habitat, they, not unsurprisingly, forage differently because abundances and distributions of food items would undoubtedly be dissimilar. The basic question that then can be asked is why the birds seek food in different portions of the habitat. This alternative does little in terms of explaining the reasons for the observed differences. To answer this, one is left to ponder the other two alternatives.

SUMMARY

Variation in foraging behavior between male and female Yellow-rumped Warblers (Dendroica coronata) was examined during the breeding season in a mixed-coniferous forest, White Mountains, Arizona. Of seven foraging variables analyzed, the male and female Yellow-rumped Warblers displayed no significant differences (G-statistic, $P > 0.05$) in method, perch type, perch diameter, or in distance from the branch tip. However, pronounced significant differences ($P < 0.05$) in foraging behavior were noted for tree species selection, and for the correlated variables tree height preference and foraging location with respect to distance from the ground. Males tended to forage in taller trees and at a greater distance from the ground. Females spent considerably more time in Douglas-fir than did males. Most
of the variation in foraging behavior may be attributable to males foraging in the vicinity of song posts, whereas females spent a greater proportion of time nearer the nest-sites.

Of the three possible alternatives examined to account for these differences, it appears that the alternative reflecting related energy savings gained by each member of the pair concentrating its foraging activities near the location of its most important reproductive duties, is the most persuasive. This alternative is also the one most closely aligned with optimal foraging theory.

ACKNOWLEDGMENTS

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LITERATURE CITED


PATTERNS OF SPACE USE IN GRASSLAND BIRD COMMUNITIES DURING WINTER

JOSEPH A. GRZYBOWSKI

Spatial relations of birds are the result of responses by individuals to various features of the environment (Brown and Orians 1970). Specific environmental features, such as nesting or roosting sites, or the amount of cover, can influence the use of space by individuals (Davis 1973, Post 1974, Snapp 1976, Pulliam and Mills 1977). Space use patterns often reflect the abilities of birds to defend and locate food or other resources (Stenger 1958, Cody 1971, Schoener 1971, Krebs 1973), avoid predation (Pulliam 1973, Bertram 1978, Kenward 1978), and interact with other individuals (Krebs 1971, Myers et al. 1979). Flocking may simultaneously enhance food exploitation and predator detection (Pulliam 1973, Powell 1974). However, Goss-Custard (1970) and Caraco (1979) pointed out that group membership may have disadvantages, such as increasing susceptibility to disease or parasites, foraging interference, and increasing costs associated with intraspecific aggression. Thus, space-use patterns of birds reflect a balance of selective forces acting both to draw organisms together and spread them apart.

This paper describes the various types of spatial occupancy used by passerine birds in open grasslands during winter, and assesses some potential mechanisms influencing these spatial relations. Grassland habitats provide a relatively simple homogeneous setting compared to scrub and woodland habitats in which factors affecting extremes in space use can simultaneously be assessed. Granivory is the primary foraging mode of grassland birds during winter (Pulliam 1975), further simplifying the system. Climatic severity and reduced winter daylength necessitate effective exploitation of food resources. While most passerines are territorial during the breeding season, the constraints of reproduction are not present during winter.

METHODS

Grasslands of varied grazing pressure or cultivation practices in several regions of Oklahoma and Texas were used. Data were collected at 14 sites from the winters of 1975–76 through 1978–79. The sampling period began 15 November and ended 15 February for each season. One Oklahoma site was also sampled in January and February 1975. The sites included seven in central Oklahoma (Cleveland, Grady, and McClain counties), three in western Texas (Muleshoe National Wildlife Refuge, Bailey County), and four on the Rob and Bessie Welder Wildlife Refuge (San Patricio County) in southern coastal Texas. The sizes of sites ranged from about 30 ha on the smallest sites in southern Texas to greater than 100
ha. Sites were characterized by their uniformity and large size, thus minimizing edge effect with other habitats. Two of the southern Texas sites contained about 5% shrub cover. Otherwise tree or shrub cover were absent or comprised less than 0.5% cover, consisting of isolated individual plants less than 3 m in height.

Sites were classified on the basis of grazing pressure or cultivation practices. A site was considered a lightly grazed grassland (LG) when the dominant palatable grasses had uniformly grown to heights approaching their maximum potential heights. For LGs in Oklahoma and southern Texas, maximum vegetation heights ranged from 1–2 m. In western Texas, maximum grass heights of LGs were about 0.5 m. When dominant palatable grasses occurred in distinct clumps, the site was designated a moderately grazed grassland (MG). Vegetation heights of MGs were up to 1 m in Oklahoma, and 1.5 m in southern Texas. When the dominant palatable grasses were absent, or present only in widely scattered clumps and/or grazed to near ground level, the site was considered a heavily grazed grassland (HG). Vegetation heights in HGs were less than 0.5 m on all sites. The cultivated sites were planted with winter wheat (*Triticum aestivum*); these sites had been harvested of a sorghum (**Sorghum bicolor**) crop in fall. On one cultivated site, only the heads of the sorghum were removed; the field was left fallow in this condition for the winter observation period. More detailed site descriptions are given in Grzybowski (1980).

Habitat height (HHT) and habitat density (HDEN) represent the primary habitat gradients present in the grasslands studied (Grzybowski 1980). Vegetation height for a 15-m² block was the average of four point samples about 1 m apart, and measured to the nearest centimeter. HDEN is:

$$\text{HDEN} = \sum_{m=1}^{4} \sum_{k=1}^{25} x_{km}$$  \hspace{1cm} (1)

where \(x_{km}\) is the number of vegetation contacts made with the tip of a wire passed through the vegetation for 30 cm at the \(k\)th height (at 10-cm intervals from 5–245 cm), and \(m\)th point (of four).

Habitat preferences were determined in the 1975–76 and 1976–77 seasons for each species on each specific grazing treatment (Grzybowski 1980). Strips 1000 × 60 m were established on each site, and these divided into 15-m² blocks. Frequency occurrence of bird species in the blocks was recorded during visits to each treatment type. The habitat values for a species on a given site were determined by averaging the HHTs and HDENs of blocks in which the species was observed. Each block used by a bird species was weighted by the frequency occurrence of that species in the block. Additional habitat sampling was conducted to characterize Horned Lark (see Table 1 for scientific names) and Chestnut-collared Longspur habitats on a HG in western Texas during the 1977–78 and 1978–79 seasons. Thirty samples, measured as above, were obtained at locations from which these species were flushed, and averaged to provide values of the habitats used.

Maps were created for five Oklahoma, two southern Texas and two western Texas sites. Flushing and landing points of birds were recorded on site maps to document space use. These points were plotted by triangulation with a single row of stakes marking the grid-blocks or with other landmarks. Only observations made on the first pass through a site were used to avoid recording space use affected by the observer.

Individual distance (IDIS) was used as a measure of spacing. The IDIS was estimated for pairs of individuals encountered on the ground or recently flushed: (a) in body lengths for distances less than 1.5 m; (b) to the nearest 0.5 m for distances less than 5 m; and (c) to the nearest meter for distances greater than 5 m. The distances to the nearest individual were obtained through direct observation or by walking spirally around the bird's flush point to 25 m (or more in a few cases) until another individual was encountered. When the nearest individual was not a conspecific, the distance to the nearest conspecific was also obtained.
Distinctions were made in western Texas among HGs grazed by cattle and those grazed primarily by prairie dogs (<i>Cynomys</i> sp.; PD). Observations made in January 1979 were separated from those made in the 1976–77 through 1977–78 seasons for a HG in western Texas; the site was ungrazed in 1978 and was in its initial stages of recovery in January 1979. Also, in January 1977, densities of LeConte’s Sparrows on a LG in southern Texas were seven times higher than the next highest estimate (Grzybowski 1982) and far above what previous investigators had encountered (Emlen 1972; G. Blacklock, pers. comm.). Observations of LeConte’s Sparrows on this site were separated from the others for analysis.

**RESULTS**

Mean values of IDIS, HHT, and HDEN for each species by grazing treatment and region are given in Table 1. Simple correlation coefficients of IDIS with HDEN and HHT were significant \( r = 0.57, P < 0.05 \). Horned Larks and Lapland Longspurs, which occupied the most open habitats, maintained mean individual distances of 2 m or less. Other gregarious species such as Chestnut-collared and Smith’s longspurs and Vesper Sparrow, which occurred in habitats with intermediate cover values, maintained mean individual distances of 3–8 m (exceptionally 12.7 m). For most grassland sparrows, however, mean IDIS was normally greater than 11 m, and in entirely solitary species, was greater than 17 m. These sparrows most often occurred in the habitats with the highest cover values.

Space-use patterns exhibited by grassland birds are summarized in Fig. 1. Each square represents an area which is large relative to the individual bird. Space-use patterns vary from those of the LeConte’s Sparrow (Type 1), where individuals appear territorial, to those of species like Lapland Longspurs (Type 4b), where individuals use large continuous areas, but where the distribution of individuals at any time is highly clumped. Patchy use of grassland habitats is exhibited by gregarious species (Type 4a) and solitary species (Type 2b). Each type is discussed below.

LeConte’s Sparrows were solitary. On a LG in central Oklahoma, they could regularly and predictably be located within particular 15-m-blocks. Their locations, made from plots of their flush routes taken from December 1975 through February 1976, strongly implicate active spacing mechanisms, and perhaps territoriality. On one southern Texas site which supported a very high density of LeConte’s Sparrows, spacing patterns were so regular in some patches that as many as 12–17 different birds (three occasions) were flushed, one every five to seven steps.

Baird’s and Grasshopper sparrows were also solitary on LGs in western and southern Texas, respectively, and exhibited spacing patterns of type 2a (Fig. 1). Distances flushed by Baird’s Sparrows were more than triple those for other solitary species (unpubl.). Of 14 initial flushes of Baird’s Sparrows, three birds flew to landing positions beyond the resolution of the observer watching with 7 × 35 binoculars. On one occasion, a Baird’s Sparrow landed within 5 m of a second sparrow. Both flushed in opposite
### Table 1

**Mean Values of Individual Distance and Habitat Density and Height for Grassland Bird Species by Region and Treatment**

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Region</th>
<th>Individual distance</th>
<th>Habitat density</th>
<th>Habitat height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horned Lark (Eremophila alpestris)</td>
<td>CU</td>
<td>Okla</td>
<td>1.7</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>LG</td>
<td>WTex</td>
<td>1.8</td>
<td>30.8</td>
<td>21.6</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>WTex</td>
<td>2.2</td>
<td>10.0</td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td>PD</td>
<td>WTex</td>
<td>1.6</td>
<td>4.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Savannah Sparrow (Passerculus sandwichensis)</td>
<td>LG</td>
<td>Okla</td>
<td>13.2</td>
<td>47.5</td>
<td>45.1</td>
</tr>
<tr>
<td></td>
<td>MG</td>
<td>Okla</td>
<td>100.0</td>
<td>32.3</td>
<td>40.6</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>Okla</td>
<td>18.7</td>
<td>38.6</td>
<td>23.8</td>
</tr>
<tr>
<td></td>
<td>LG</td>
<td>STex</td>
<td>6.9</td>
<td>52.0</td>
<td>60.1</td>
</tr>
<tr>
<td></td>
<td>MG</td>
<td>STex</td>
<td>14.1</td>
<td>52.0</td>
<td>60.1</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>STex</td>
<td>12.2</td>
<td>28.4</td>
<td>23.3</td>
</tr>
<tr>
<td>Grasshopper Sparrow (Ammmodramus savannarum)</td>
<td>MG</td>
<td>STex</td>
<td>19.5</td>
<td>68.8</td>
<td>63.6</td>
</tr>
<tr>
<td>Baird’s Sparrow (Ammmodramus bairdii)</td>
<td>LG</td>
<td>WTex</td>
<td>60.7</td>
<td>30.0</td>
<td>21.6</td>
</tr>
<tr>
<td>LeConte’s Sparrow (Ammmodramus leconteii)</td>
<td>LG</td>
<td>Okla</td>
<td>42.7</td>
<td>66.4</td>
<td>63.2</td>
</tr>
<tr>
<td></td>
<td>LG</td>
<td>STex</td>
<td>11.1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>MG</td>
<td>STex</td>
<td>17.1</td>
<td>64.0</td>
<td>63.2</td>
</tr>
<tr>
<td>Vesper Sparrow (Pooeetes gramineus)</td>
<td>MG</td>
<td>STex</td>
<td>3.7</td>
<td>37.7</td>
<td>24.6</td>
</tr>
<tr>
<td>Lapland Longspur (Calcarius lapponicus)</td>
<td>CU</td>
<td>Okla</td>
<td>1.5</td>
<td>0.6</td>
<td>1.0</td>
</tr>
<tr>
<td>Smith’s Longspur (Calcarius pietus)</td>
<td>MG</td>
<td>Okla</td>
<td>2.9</td>
<td>33.5</td>
<td>39.0</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>Okla</td>
<td>2.9</td>
<td>37.7</td>
<td>21.2</td>
</tr>
<tr>
<td>Chestnut-collared Longspur (Calcarius ornatus)</td>
<td>MG</td>
<td>Okla</td>
<td>5.4</td>
<td>29.3</td>
<td>38.7</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>Okla</td>
<td>6.5</td>
<td>25.5</td>
<td>17.3</td>
</tr>
<tr>
<td></td>
<td>HG</td>
<td>WTex</td>
<td>12.7</td>
<td>15.5</td>
<td>14.5</td>
</tr>
<tr>
<td></td>
<td>HG*</td>
<td>WTex</td>
<td>7.6</td>
<td>17.6</td>
<td>14.5</td>
</tr>
</tbody>
</table>

* CU = cultivated; HG = heavily grazed; LG = lightly grazed; MG = moderately grazed; PD = prairie dog town.

\* Okla = Oklahoma; STex = southern Texas; WTex = western Texas.

* Means from January 1979 when the site was recovering from being heavily grazed.

Savannah Sparrows were variable in the use of space. They exhibited type 2b spacing patterns (Fig. 1) on a LG in central Oklahoma where distinct patches with lower vegetation height and density than the site means (Fig. 2) were regularly used. Only one bird/patch occurred in the smallest patches. Birds in patches occupied by more than one individual were normally solitary, but flew near each other when disturbed. On MGs
in Oklahoma, where patchiness of habitat was not distinctive, birds exhibited type 2a spacing patterns similar to Baird’s Sparrows in western Texas.

On some sites, where Savannah Sparrow densities were high, the type 3 spacing pattern (Fig. 1) was observed. Savannah Sparrows were widely spaced when first encountered with mean inter-individual distances of 7–14 m (Table 1), but often joined in groups when disturbed. These groups would continue to grow in numbers as I progressively chased birds about the area and would travel circular paths within certain bounds. Fig. 3 shows areas occupied by groups of sparrows on an Oklahoma site. On a southern Texas site where densities were very high, the paths of groups overlapped and could not clearly be defined. These groups may have been composed of different combinations of individuals for each observation, their composition dependent on the path of movement of the observer.

On one Oklahoma site, about 30 Savannah Sparrows, which formed into a group when disturbed by the observer, could be chased to the edge of their cover, where they circled back and dispersed as solitary birds. A repeat performance occurred in 0.5 h, when all birds were dispersed singly. Basically, Savannah Sparrows on this site maintained solitary behavior except when disturbed.

Smith’s and Chestnut-collared longspurs were gregarious but frequent ed specific patches of a grassland site (Type 4a; Fig. 1). Use by Smith’s Longspurs on a HG in central Oklahoma appeared to favor particular patches with vegetation heights lower than the site mean (Fig. 4A) but with moderate to low vegetation densities (Fig. 4B). These patches generally contained dense growth of three-awn (*Aristida* sp.), a short flimsy grass species, and silver beardgrass (*Andropogon saccharoides*). Chestnut-collared Longspurs occurred mostly in pockets of sparser, but similar vegetation (Fig. 4A, B) between areas used by Smith’s Longspurs. Smith’s Longspurs, observed on two sites, also favored dense patches of three-awn and silver beardgrass (pers. obs.). Chestnut-collared Longspurs observed on MGs, where no other longspur species occurred, used particular areas extensively during one winter season (unpubl.).

Lapland Longspurs and Horned Larks exhibited type 4b spacing patterns (Fig. 1). Lapland Longspurs on most cultivated sites in central Oklahoma, and Horned Larks on a prairie dog town in western Texas occupied extensive and continuous areas of their site. However, at any one time their distributions were clumped. They were often observed flying overhead from most grassland sites, and often from non-grassland sites in loosely spaced groups.

In western Texas during two years of the study, Chestnut-collared Long spurs exhibited type 2c spacing pattern (Fig. 1). Birds were widely scattered during the day (08:30–16:00). One very widely spaced group of 16
SPACE USE PATTERNS OF GRASSLAND BIRDS

Fig. 1. Diagramatic representation of spacing patterns exhibited by grassland birds during winter. Four types are identified. Each square represents an area which is large relative to the individuals. Individuals are represented by dots; six dots in each square are used for convenience. Solid circles surrounding dots in type 1 represent use-areas to which enclosed individuals (dots) restrict themselves. Circles formed with dashed lines represent temporary use areas. Three sizes of circles are used—the smallest for types 4a and 4b represent areas of individual distance; intermediate in types 1, 2b, and 3 represent "territories" or individual spacing units larger than individual distances; and the largest for type 3 represents an area of group activity. Ellipses (in types 2b and 4a) represent patches of preferred habitat. Arrows depict the magnitude of potential movements by individuals, including within "territories."
Fig. 2. Distribution of vegetation heights used by Savannah Sparrows as they deviate from the distribution of a random sample on a lightly grazed grassland in central Oklahoma during the winter of 1975–76. Mean vegetation height is 61.5 cm.

was located (in 19 days of observation), in addition to other groups of 5, 7, and 11 individuals. All other observations were of one or two birds. Seed abundance was low compared to other sites (Grzybowski 1982, 1983), and may account for the solitary foraging behavior of these birds. In January 1979, one or two groups of Chestnut-collared Longspurs (numbering from 18–30) were located on a heavily grazed site in patches where three-awn was conspicuous; they exhibited type 4a spacing patterns (Fig. 1). Seed density was also higher in these patches than in other areas where single birds occurred (Grzybowski 1982, 1983).

DISCUSSION

Passerines occupying grasslands exhibit territorial defense in spacing themselves during the breeding season (Cody 1968, Murray 1969, Wiens (type 1), locally within site (type 2a), within and between patches (types 2b and 4a), within group activity areas (type 3), within site (types 2c and 4b), and between sites (types 2c, 4a, and 4b).
In winter, only LeConte's Sparrows in Oklahoma exhibited spacing patterns resembling territories; but this spacing behavior may be the result of avoidance rather than active defense. However, evidence is indirect. Many individuals on a southern Texas site, when bird densities were extremely high, were uniformly spaced about 6 m apart. In addition, grasslands used by LeConte's Sparrows were often seed-poor (Grzybowski 1982, 1983); defense of areas on these sites may cost more in energy than the resource base can support. LeConte's Sparrows may need to conserve energy just to occupy these grasslands. Crops of LeConte's Sparrows collected in southern Texas rarely contained more than 20 seeds, even at dusk, compared to 200 or more seeds in crops of Savannah Sparrows (unpubl.), further implicating the impact of low seed availability and energy conservation for LeConte's Sparrow.

Because avoidance behavior is a subtle process compared to overt aggression, it has been little studied. Waser (1976) found that groups of gray-cheeked mangabeys (Cercocebus albigena) avoided each other. East-
ern chipmunks (*Tamias striatus*) maintain overlapping territories defended from non-territorial intruders; however, established neighbors avoided encountering each other on overlapping portions of their territories (Getty 1981). In birds, this process has not been demonstrated.

More commonly, grassland birds were not as restrictive or exclusive in their use of space as LeConte’s Sparrows. Species such as longspurs were highly gregarious and mobile (Grzybowski 1983). They occupy exposed grasslands with moderate to high seed densities. Gregariousness of longspurs in these habitats may serve in enhancing early predator detection (Caraco 1979). Gregarious species occurred in habitats with low or inter-
mediate HDEN. Solitary passerines never occurred in sparsely vegetated grasslands.

Lapland Longspurs and Horned Larks occurred in the sparsest grassland habitats with almost no cover. Lapland Longspurs form large groups, and Horned Larks in November (pre-breeding) were primarily flockers. Chestnut-collared Longspurs observed in migration in plowed fields were also seen in large groups. Large flocks in open terrain may be useful in flocking maneuvers which evade avian predators or increase the predator's risk of collision with non-target birds (Treisman 1975). I observed Prairie Falcons (*Falco mexicanus*) attempting to capture these species on four occasions; the falcons flew low toward a flock. These longspurs and larks all flew up in response to a falcon, forming into a tight group. Horned Larks responded similarly to Burrowing Owls (*Athene cunicularia*) accidentally flushed by the observer into the flocks.

The attraction of grassland birds to sites with higher seed densities may make it impossible for individuals to maintain territorial defense against intruders. Myers et al. (1979) observed this condition in Sanderlings (*Calidris alba*) using areas of high prey density. In open grasslands, the combination of exposure to predation, which clusters birds, exposure to weather, which increases energy demands, and the attraction of more individuals to sites with higher seed densities, creates a situation where seeds can be locally exploited. This may impose the need for a mobile and energetically more costly strategy, where groups look for patches or sites (which could be considered patches for larger groups) with seed densities high enough to support groups and compensate the energy requirements necessary to find the patches. This process of patch use may be a variation of risk-aversion flocking described by Caraco (1980) and mediated by the need of birds in exposed habitats to form groups which enhance predator detection and increase an individual's foraging time (Caraco 1979). These conditions may preclude territorial space use patterns for grassland birds during winter, and encourage intra- and intersite mobility.

A potential compromise between the advantages and disadvantages of flocking is found in Savannah Sparrows. At moderate to high bird densities, Savannah Sparrows clustered in only part of their habitat use area at any time (Fig. 1, Type 3), but were spaced apart at 12-14 m. The data of first-disturbed birds indicate that Savannah Sparrows have evolved spatial and social habits which take advantage of spacing birds apart, yet still have positive group effects. This may be a very flexible system in which sparrows use the level of disturbance by potential predators to adjust individual distance in such a way that the benefits of predator detection are enhanced while the costs of flocking are reduced.

Pulliam and Mills (1977) presented evidence that space use by grassland
sparrows may be affected by the presence of tree or shrub cover. According to these authors, competing species vie for positions near cover to enhance predator avoidance. Pulliam and Mills (1977) claimed that Savannah Sparrows are displaced from tree or shrub cover by Vesper Sparrows. In Fig. 3, however, only two of the four group ranges of Savannah Sparrows included cover greater than 1 m tall, in spite of the presence of this cover nearby and the absence of other sparrow species. In general, Savannah Sparrows avoided habitats with vegetation heights greater than 1 m unless they were disturbed repeatedly.

SUMMARY

The use of space by grassland birds during winter is variable, but generally exhibits patterns which indicate high intra- and intersite mobility. Only the LeConte’s Sparrow exhibited space use resembling territories, but these may be maintained by avoidance rather than defense. Individual distance was inversely correlated \( (P < 0.05) \) with habitat height and habitat density. Social behavior enhancing predator detection appears to be an important factor influencing the use of space by grassland birds.

ACKNOWLEDGMENTS

This research was partially funded by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Oklahoma Ornithological Society, and the Research Council of the University of Oklahoma. Computer facilities were provided by the University of Oklahoma Computer Services. My thanks go to D. Wynne, H. Myser, W. Shokey, F. McCormick, W. Johnson, W. Goldsmith, and S. Barbour for graciously allowing me access to their property. I also thank other unknown landowners whose grasslands I traversed. I extend my appreciation to B. Henderson for permitting me to use properties of the University of Oklahoma and to the U.S. Fish and Wildlife Service and the personnel at Muleshoe National Wildlife Refuge for use of their lands and facilities. I especially thank B. Long for his companionship and occasional meals during my stays at Muleshoe. I also thank the personnel at Welder Wildlife Foundation, including E. Bolen, L. Drawe, F. Glazener, J. Teer, G. Blacklock, and C. Valenueva, for the use of their facilities. Special thanks go to E. Bolen for his helpfulness. I thank my wife, Eileen, for her devoted support. Finally, I extend my gratitude to G. D. Schnell for use of his laboratory, facilities, and personal office. C. C. Carpenter, J. R. Estes, J. D. Rising, G. D. Schnell, B. M. Vestal, J. A. Wiens, and an anonymous referee provided useful comments for improving earlier drafts of this paper.

LITERATURE CITED


DEPT. ZOOLOGY AND OKLAHOMA BIOLOGICAL SURVEY, UNIV. OKLAHOMA, NORMAN, OKLAHOMA 73019. (PRESENT ADDRESS: EVANS HALL, CENTRAL STATE UNIV., EDMOND, OKLAHOMA 73034.) ACCEPTED 29 APR. 1983.
AN ANALYSIS OF BODY MASS, WING LENGTH, AND VISIBLE FAT DEPOSITS OF DARK-EYED JUNCOS WINTERING AT DIFFERENT LATITUDES

Val Nolan Jr. and Ellen D. Ketterson

During winter, many bird species at temperate latitudes increase their stored fat (see King and Farner 1966, King 1972 for review of older literature; O' Connor 1973, Evans and Smith 1975, Biebach 1977, Vincent and Bédard 1976, Carey et al. 1978, Blem 1978 for more recent findings). Winter fattening is considered an adaptive response to the increases in thermoregulatory costs, duration of nocturnal fasting, and risk that in severe climates snow or ice storms will curtail or prevent daylight feeding.

If climate (including day length) is the ultimate cause of winter fattening, then in much of the world populations of the same species wintering at different latitudes should differ in amount of fat stored (King and Mewaldt 1981). In certain sedentary species, higher body mass (wet weight) and thus perhaps greater fat stores have been found to be characteristic of more northern populations (e.g., the Great Tit [Parus major], compare van Balen 1967 and Haftorn 1976; and the House Sparrow [Passer domesticus] Blem 1973); but studies of migratory birds have produced conflicting results. Several species of shorebirds exhibit the expected trend (Pienkowski et al. 1975, Dick and Pienkowski 1979), but neither White-crowned Sparrows (Zonotrichia leucophrys gambelii) (King and Mewaldt 1981) nor American Goldfinches (Carduelis tristis) (Wiseman 1975, Carey et al. 1978) are heavier farther north. The European Starling (Sturnus vulgaris), a partial migrant, exhibits still a different pattern, carrying more fat at mid-latitudes than it does to the north or south (Blem 1981).

In this paper we analyze, according to sex and age, variation in body mass of 1835 migratory Dark-eyed Juncos (Junco hyemalis) from six wintering locations in the eastern United States. Juncos have been the subject of numerous studies of body mass in the laboratory and field (Helms and Drury 1960, Johnston 1962, Weise 1963, Farrar 1966, Helms et al. 1967, Knowles 1972, Swanson 1975, Holmes 1976, Prescott 1978), but sex and/or age was not determined in most of these. Juncos are known to fatten in winter (Helms et al. 1967, Bower and Helms 1967, Holmes 1976); and in one geographic comparison, mass was greater at a higher latitude (Massachusetts) than at a lower (Delaware), even when temperatures were warmer at the more northerly location (Helms and Drury 1960, Knowles 1972). Here we ask whether body mass varies with latitude and whether any variation that is found can be attributed to differences in fat storage.
We also consider possible advantages of fatness and leanness to wintering juncos, as well as what environmental cues might elicit (or suppress) fattening and thus account for any geographic patterns that exist.

METHODS

**Sampling.**—Locations and dates of sampling appear in Table 1 (for further details, see Ketterson and Nolan 1982). Early-winter sampling (on or before 9 January) was carried out during 2-5 winters in Michigan (N = 5), Indiana (N = 2), Tennessee (N = 3), South Carolina (N = 4), and Alabama (N = 2). Late-winter sampling (2 February–15 March) took place during one to two winters in Indiana (N = 2), Tennessee (N = 1), South Carolina (N = 2), and Mississippi (N = 1). Michigan and Indiana we refer to as northern, and other locations we regard as southern.

Subjects were captured, usually by netting, at sites baited with millet and cracked corn. They were banded, weighed to the nearest 0.1 g (50 g Pesola spring balance), measured (flattened wing), and sexed by methods previously described (Ketterson and Nolan 1976, 1982). Age was determined by examining skull pneumatization and/or a combination of eye color and plumage traits in early winter, by eye color, plumage, and wing length in late winter. Birds were categorized either as having hatched during the preceding breeding season (hereafter, young) or in an earlier season (adult). Reliability of aging approached 100% in early winter; it was slightly greater than 90% in late winter, as we determined by re-aging at that time juncos whose skulls had been examined in November and December (Ketterson and Nolan 1982). Most weights were taken within 1 h of capture, none more than 2 h after capture. Visible fat was classified using a modified version of the scale of Helms and Drury (1960): 0 = no fat on abdomen (A) or in furcula (F); 1 = F < 33% full, A < 50% covered; 2 = F 33–66% full, A 50–100% covered but surface not even with pectoral region; 3 = F filled, A covered and flush with pectoral region, neither A nor F bulging; 4 = either F or A bulging; 5 = both F and A bulging. Scoring was done before weighing and therefore was not influenced by results of weighing. Because we did not begin to score fat until midway in the study, this data set is smaller than that for body mass. Sampling efforts lasted several days each time we visited a particular location; when juncos were caught more than once during an effort, only the mass at first capture was included in the analysis.

**Environmental data.**—Air temperatures before and during sampling were determined from Climatological Data (1976–1980, U.S. Weather Bureau). Reporting stations were within 16 km of their respective sampling locations. “Prior temperature” is the mean of daily mean ([maximum + minimum]/2) temperatures during the 3 days immediately preceding the first day of sampling. “Immediate temperature” is the mean of daily means on the days on which we sampled. “Day length” is the period between morning and evening civil twilight (Nautical Almanac, 1981). From our field observations we characterized snow as falling, on the ground but not falling, or absent. These environmental data appear in Table 1.

**Data analysis.**—Statistical analyses were done using the Statistical Package for Social Sciences (SPSS, Nie et al. 1975). A three-way analysis of variance was employed to analyze the effect in early winter of sex, age, and location on body mass and wing length. First we tested both dependent variables for heterogeneity across years; using one-way ANOVAs of mass and wing length by year, each sex-age class was treated separately at each location (Table 1 shows data in summary form). Wing lengths were homogeneous except that adult males in Michigan were smaller in the first year of the study than thereafter. Body weight exhibited heterogeneity in the following instances: in Michigan and Indiana (adult and young males, young females), Tennessee (adult females), and South Carolina (young males, adult females). Despite heterogeneity, we combined data across years because a four-way analysis
of variance (one that partitioned among years) was prohibited by the fact that sites were sampled in unequal numbers of years. We justified this pooling on two grounds. First, in every year Michigan and Indiana juncos of each class were significantly heavier than birds of the same class from the southern locations. Therefore, the latitudinal difference in body mass that we report below did not arise out of any tendency to sample northern (or southern) juncos in years when juncos everywhere tended to be heavier (or lighter). Second, the almost uniform absence within a sex-age class of annual variation in wing length at each location suggested to us that juncos at any particular site were similar in lean mass from year to year and that only their fat stores differed. From the many options in SPSS three-way ANOVAs, we selected the classic analysis in which each main effect is assessed separately, adjusting for the effect of every other, before assessing the effects of two-way and then three-way interactions (Nie et al. 1975:415).

Visible fat class data were analyzed by Chi-square. Because these sample sizes were smaller than the others, we combined cases from the southern localities and compared them with those from the combined northern localities.

Environmental influences on body mass of each sex-age class were assessed by standard multiple regression (Nie et al. 1975:336), treating each individual as a case. Snow cover was a dummy variable and was coded 0 for no snow and 1 for snow falling or on the ground.

RESULTS

Total body mass and latitude.—Fig. 1 presents, according to latitude of capture site, the mean body mass of each sex-age class in early winter (N = 1353, all years). As Fig. 1 shows, juncos wintering in Tennessee, South Carolina, and Alabama were of similar mass; north of 36°N (Tennessee), mass increased with latitude. Further, males were considerably heavier than females and adults were slightly heavier than young. Three-way analysis of variance confirms these trends as statistically significant and quantifies the differences as follows (Table 2): after correcting for age and location, males were 1.24 g heavier than females; after correcting for sex and location, adults were only 0.26 g heavier than young; after correcting for sex and age, Michigan juncos were 2.73 g heavier than Alabama juncos. We limited this analysis (and those that follow, except where stated) to early winter because aging was more reliable at that season and because Michigan was sampled only at that time. Late-winter results (see Table 1), however, also indicate a latitudinal difference: Indiana juncos were significantly heavier than those from southern sites (results not shown, three-way ANOVA).

This north–south variation in total body mass (wet weight) obviously arose out of differences in one or more of the components of total body mass, including lean mass, fat, body water, and crop contents; and we now consider how these components may have varied geographically.

Lean body mass, as reflected by wing length.—Wing length is almost certainly not a perfect correlate of lean mass, although it is widely used (e.g., James 1970) as such when fat extraction is impossible. Among female juncos, fat extraction has demonstrated a significant correlation between
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<th>Symbol</th>
<th>Dates</th>
<th>Prior temp. (°C)</th>
<th>Immediate temp. (°C)</th>
<th>Day length (h)</th>
<th>Snow</th>
<th>Adult males</th>
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<td>19.41 ± 0.248</td>
<td>17.37 ± 0.260</td>
<td>18.01 ± 0.231</td>
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Table 1: Dates of Capture, Selected Environmental Conditions, and Body Mass by Sex-Age Class during Each Capture Effort.
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<td>Adult males</td>
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* See text for definitions and methods of determining environmental conditions.
* Symbols are those used in Fig. 4 and are given to permit cross reference.
* Standard error follows mean. Sample size in parentheses.
lean mass and wing length (Helms et al. 1967), and we have found (unpubl.) a significant positive relationship between wing length and other measures that may correlate with lean mass: tarsal length, tail length, and several bill dimensions. Accordingly, we analyzed early-winter wing length within each sex-age class, from north to south. (Use of wing length was not necessary in early winter, either for the purpose of sexing or of aging.) Fig. 2 and Table 2 show that there were no within-class geographic differences in early winter when all years were combined (N = 1692), and this was also true during each year (results not shown, one-way ANOVA).

The similarity in wing length among juncos of the same sex and age,
<table>
<thead>
<tr>
<th>Main effects</th>
<th>Body mass</th>
<th>Wing length</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sex</strong></td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Male</td>
<td>850, 0.46 g</td>
<td>1074, 1.60 mm</td>
</tr>
<tr>
<td>Female</td>
<td>503, -0.78 g</td>
<td>618, -2.79 mm</td>
</tr>
<tr>
<td><strong>Age</strong></td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Adult</td>
<td>635, 0.14 g</td>
<td>795, 0.89 mm</td>
</tr>
<tr>
<td>Young</td>
<td>718, -0.12 g</td>
<td>897, -0.79 mm</td>
</tr>
<tr>
<td><strong>Location</strong></td>
<td>***</td>
<td>NS</td>
</tr>
<tr>
<td>Michigan</td>
<td>559, 1.43 g</td>
<td>697, 0.04 mm</td>
</tr>
<tr>
<td>Indiana</td>
<td>159, -0.19 g</td>
<td>283, 0.06 mm</td>
</tr>
<tr>
<td>Tennessee</td>
<td>145, -1.19 g</td>
<td>177, 0.18 mm</td>
</tr>
<tr>
<td>South Carolina</td>
<td>410, -1.21 g</td>
<td>453, -0.13 mm</td>
</tr>
<tr>
<td>Alabama</td>
<td>80, -1.30 g</td>
<td>82, -0.18 mm</td>
</tr>
<tr>
<td><strong>Interactions</strong></td>
<td>NS</td>
<td>***</td>
</tr>
<tr>
<td>Sex-age</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Age-site</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Sex-age-site</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

\(r^2\) 0.549 0.834

Grand mean 19.90 g 80.13 mm

### Table 2
Three-way ANOVA Comparing Body Mass and Wing Length in Early Winter by Sex, Age, and Location

* Asterisks indicate results of F-tests (***, \(P < 0.001\); **, \(P < 0.01\); *, \(P < 0.05\)) for main effects (sex, age, location) and interactions; NS indicates \(P > 0.05\). Also given are sample size for each category (e.g., male) separated by a comma from the average deviation in mass of the members of that category from the grand mean (mean of all individuals regardless of category, see bottom line of table) after adjusting for the other main effects. For example, we analyzed body mass of 1353 juncos and the grand mean was 19.9 g; 850 of these were male, and males tended to exceed the grand mean by 0.46 g after accounting statistically for variation in mass attributable to age and capture location. Similar data have been presented for wing length, but because there was a significant sex-age interaction the deviations must be considered only an approximation.

regardless of wintering site, makes it appear highly improbable to us that the demonstrated differences in overall mass were primarily attributable to variation in lean body mass.

Fat stores, as reflected by visible subcutaneous fat.—Fat classes of northern juncos tended to be much higher than those of southern juncos (Fig. 3 and Table 3). We conclude, therefore, that at least some of the greater overall mass of northern juncos was attributable to their carrying more fat, and in most of the remainder of this paper we seek to account for that difference.

Other possible sources of variation.—It is possible that northern juncos
carried more body water, and it seems probable that their crop contents were greater. Our bait provided abundant food at all capture sites, but southern juncos may have eaten less frequently and/or consumed less during a single feeding bout. The extent to which these components contributed to the geographic variation in total mass is not known.

Environmental correlates of body mass.—In an effort to explain the north–south variation in fat stores, we regressed (multiple regression) body mass on four environmental and two temporal variables as well as on latitude and wing length. Early- and late-winter data were combined and the sex-age classes analyzed separately. Table 4 presents the results.
Latitude accounted for most of the explained variation. Juncos of each sex-age class were heavier at higher latitudes, and this was true even after controlling statistically for climatic factors often thought to affect seasonal differences in fat stores, i.e., day length, presence or absence of snow, and immediate and prior temperature. Other significant partial regressions were these: (1) Mass increased with day length, i.e., juncos were heavier in late winter. (2) Mass was greater when snow was present. (3) Except in adult females, mass was negatively correlated with air temperature on the days just prior to sampling; except in young females, it was not correlated with air temperature on the days of sampling. (Fig. 4 depicts for one class, adult males, the relationship between mass and prior temperature.) (4) Mass was greater later in the day, as is commonly true (e.g., Helms and Drury 1960). (5) Mass increased with wing length. This may be taken as evidence that wing length is a good indicator of overall lean body size (see above), but other possible interpretations are that longer-winged juncos carry relatively more fat, have more body water, or have fuller crops.

Despite the use of seven independent variables in this regression, considerable variation in body mass was unexplained. Measurement error is partly responsible for this, but unidentified environmental factors may also have been important.
Table 3
Relative Frequency of Individuals Belonging to Various Visible Fat Classes\(^a\) in Early Winter, According to Location and Sex-Age Class; Southern Locations (Alabama, South Carolina, Tennessee) are Combined and Compared to Northern Locations (Michigan and Indiana) Combined\(^b\)

<table>
<thead>
<tr>
<th>Visible fat class</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>median(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>5</td>
<td>16</td>
<td>27</td>
<td>55</td>
<td>21</td>
<td>8</td>
<td>2.83</td>
</tr>
<tr>
<td>South</td>
<td>84</td>
<td>21</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.14</td>
</tr>
<tr>
<td>(\chi^2 = 171.23) df = 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>4</td>
<td>28</td>
<td>49</td>
<td>48</td>
<td>18</td>
<td>3</td>
<td>2.38</td>
</tr>
<tr>
<td>South</td>
<td>72</td>
<td>20</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>(\chi^2 = 163.17) df = 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Adult females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>2</td>
<td>3</td>
<td>7</td>
<td>9</td>
<td>6</td>
<td>1</td>
<td>2.72</td>
</tr>
<tr>
<td>South</td>
<td>103</td>
<td>21</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.12</td>
</tr>
<tr>
<td>(\chi^2 = 101.91) df = 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Young females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>3</td>
<td>5</td>
<td>14</td>
<td>16</td>
<td>8</td>
<td>2</td>
<td>2.63</td>
</tr>
<tr>
<td>South</td>
<td>88</td>
<td>17</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.10</td>
</tr>
<tr>
<td>(\chi^2 = 115.17) df = 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Visible fat was classified according to the method of Helms and Drury (1960), slightly modified as described in the text.

\(^b\) Fat classes 0, 1, 2, and 3-5 (last combined) were compared in order to produce acceptable expected values.

\(^c\) Medians were determined by linear interpolation.

Discussion

Our data indicate that (1) junco body size, insofar as it is accurately indicated by wing length, does not vary from north to south during winter; (2) junco body mass does vary, and the larger mass of northern juncos is at least in part attributable to greater fat stores; and (3) the single best predictor of mass, and thus probably of fat stores, is the latitude of the wintering site.

The absence of geographic size (wing length) variation across the winter range of a migratory species is interesting in itself, because many sedentary species in eastern North America exhibit clines in wing length that are closely correlated with climatic variation (James 1970). Similar clines could arise in a migratory species if some mechanism caused individuals to select their wintering sites according to their body sizes. Apparently, juncos have no such mechanism (see also Ketterson and Nolan 1982).

In seeking to account for variation in fat stores, most studies of fattening have focused on temporal fluctuations in fat within and across winters and
Table 4

Standard Multiple Regression of Body Mass on Latitude, Wing Length, and Environmental Variables, Early and Late Winter, According to Sex and Age

<table>
<thead>
<tr>
<th>Variable</th>
<th>Adult males</th>
<th>Young males</th>
<th>Adult females</th>
<th>Young females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b</td>
<td>Partial $F, P$</td>
<td>$r^2$ contribution</td>
<td>Simple $r$</td>
</tr>
<tr>
<td>Latitude</td>
<td>0.192</td>
<td>19.97, ***</td>
<td>0.348</td>
<td>0.590</td>
</tr>
<tr>
<td>Wing length</td>
<td>0.170</td>
<td>19.80, ***</td>
<td>0.022</td>
<td>0.154</td>
</tr>
<tr>
<td>Time</td>
<td>0.001</td>
<td>42.26, ***</td>
<td>0.051</td>
<td>0.266</td>
</tr>
<tr>
<td>Day length</td>
<td>0.307</td>
<td>7.56, **</td>
<td>0.031</td>
<td>-0.210</td>
</tr>
<tr>
<td>Snow</td>
<td>0.817</td>
<td>13.30, ***</td>
<td>0.012</td>
<td>0.587</td>
</tr>
<tr>
<td>Prior temperature</td>
<td>-0.061</td>
<td>14.51, ***</td>
<td>0.014</td>
<td>-0.552</td>
</tr>
<tr>
<td>Immediate temperature</td>
<td>0.022</td>
<td>1.14, NS</td>
<td>0.001</td>
<td>-0.524</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latitude</td>
<td>0.222</td>
<td>24.38, ***</td>
<td>0.321</td>
<td>0.567</td>
</tr>
<tr>
<td>Wing length</td>
<td>0.128</td>
<td>10.43, ***</td>
<td>0.007</td>
<td>0.086</td>
</tr>
<tr>
<td>Time</td>
<td>0.001</td>
<td>23.17, ***</td>
<td>0.024</td>
<td>0.308</td>
</tr>
<tr>
<td>Day length</td>
<td>0.496</td>
<td>18.94, ***</td>
<td>0.047</td>
<td>-0.164</td>
</tr>
<tr>
<td>Snow</td>
<td>0.633</td>
<td>6.89, **</td>
<td>0.007</td>
<td>0.559</td>
</tr>
<tr>
<td>Prior temperature</td>
<td>-0.047</td>
<td>9.24, **</td>
<td>0.008</td>
<td>-0.478</td>
</tr>
<tr>
<td>Immediate temperature</td>
<td>0.015</td>
<td>0.66, NS</td>
<td>0.000</td>
<td>-0.463</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latitude</td>
<td>0.195</td>
<td>14.14, ***</td>
<td>0.209</td>
<td>0.458</td>
</tr>
<tr>
<td>Wing length</td>
<td>0.169</td>
<td>16.05, ***</td>
<td>0.036</td>
<td>0.220</td>
</tr>
<tr>
<td>Time</td>
<td>0.001</td>
<td>19.28, ***</td>
<td>0.052</td>
<td>0.255</td>
</tr>
<tr>
<td>Day length</td>
<td>0.408</td>
<td>13.09, ***</td>
<td>0.051</td>
<td>0.037</td>
</tr>
<tr>
<td>Snow</td>
<td>0.712</td>
<td>10.63, ***</td>
<td>0.022</td>
<td>0.489</td>
</tr>
<tr>
<td>Prior temperature</td>
<td>0.008</td>
<td>0.13, NS</td>
<td>0.000</td>
<td>-0.396</td>
</tr>
<tr>
<td>Immediate temperature</td>
<td>-0.018</td>
<td>0.41, NS</td>
<td>0.001</td>
<td>-0.455</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latitude</td>
<td>0.280</td>
<td>30.68, ***</td>
<td>0.328</td>
<td>0.572</td>
</tr>
<tr>
<td>Wing length</td>
<td>0.233</td>
<td>22.25, ***</td>
<td>0.026</td>
<td>0.155</td>
</tr>
<tr>
<td>Time</td>
<td>0.001</td>
<td>10.78, ***</td>
<td>0.020</td>
<td>0.220</td>
</tr>
<tr>
<td>Day length</td>
<td>0.379</td>
<td>10.89, ***</td>
<td>0.038</td>
<td>-0.134</td>
</tr>
<tr>
<td>Snow</td>
<td>0.642</td>
<td>6.33, *</td>
<td>0.006</td>
<td>0.529</td>
</tr>
<tr>
<td>Prior temperature</td>
<td>-0.053</td>
<td>6.81, **</td>
<td>0.004</td>
<td>-0.490</td>
</tr>
<tr>
<td>Immediate temperature</td>
<td>0.052</td>
<td>5.62, *</td>
<td>0.009</td>
<td>-0.446</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

b = partial regression coefficient; $r^2$ = coefficient of determination; simple $r = Pearson's correlation coefficient.

Levels of significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS $P > 0.05$. ** Levels of significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS $P > 0.05$. b = partial regression coefficient; $r^2$ = coefficient of determination; simple $r = Pearson's correlation coefficient.
have sought to correlate these with a variety of environmental variables (e.g., King and Farner 1966, Evans 1969). These studies distinguish between proximate and ultimate causation, i.e., between (1) selective pressures that over evolutionary time have favored individuals that fatten at some dates but not at others and (2) external cues and/or internal rhythms that vary with the season and cause the animal to fatten or not. The discussion that follows makes the same distinction, but our emphasis is on spatial as opposed to temporal variation.

Ultimate cause of fattening.—The ultimate cause of the geographic variation in fat stores that we report is almost certainly climate. Weather is much more likely to restrict the food of northern than of southern juncos. When this happens, the birds can either wait out the period of severe weather, making local movements in search of exposed food, or they can engage in long-distance dispersal that might enable them to reach regions unaffected by the adverse weather. Movements on this latter scale would resemble migration in their energetic demands, and preparation to meet those demands might account for the fatness of northern juncos. However,
for two reasons we believe that northern juncos rarely make long-distance winter movements to escape food deprivation. First, analysis of United States Fish and Wildlife Service banding and recovery data reveals little within-winter long-range dispersal (Ketterson and Nolan 1982). Second, with C. M. Rogers, we have transported juncos from Michigan and Tennessee in December and released them in Indiana in January. Most remained at the release site and were recaptured, many after 6 weeks. This suggests to us that the birds may have been physiologically incapable of long movements (see also Rowan 1927); and we believe that it is the strategy of juncos to wait out bad weather at or near the location in which they settle after autumn migration, metabolizing their stored fat in the interim.

In this study, Michigan juncos were approximately 2.7 g heavier than Alabama juncos after correction for sex and age. If we use the rate of overnight weight loss, 0.11 g/h at 4°C, reported for juncos by Ketterson and Nolan (1978) to estimate fasting ability, 2.7 g translates to a 25-h north–south difference. Alternatively, Stuebe and Ketterson’s (1982) regression of body mass on fasting endurance [endurance (h) = 5.65 (initial mass [g]) − 74.30] gives Michigan juncos a 14–17-h advantage. Whichever estimate is more nearly correct, the potential advantage of carrying fat in harsh climates seems clear.

Possible advantages of leanness.—The almost uniformly low fat levels of southern juncos may be as interesting as the high levels of their northern counterparts. While it is possible that juncos in the south were lean because food was scarcer there than in the north, we think this very unlikely. First, southern juncos were, like northern, heavier in late winter than in early winter (Table 1), notwithstanding that the food of juncos is largely non-renewing in winter and undergoes depletion with time. Second, recalling that the sex-age classes of juncos differ in relative dominance status and that adult males are the dominant class (Balph 1977, Baker and Fox 1978, Ketterson 1979), we would expect, in the event of food shortage, that adult males would suffer least and therefore would carry the most fat. Contrary to this expectation, Table 3 shows that the median fat classes in early winter in the south were similar for all sex-age classes, suggesting no inequality of access to scarce resources. We therefore believe that southern juncos were lean because it was advantageous to be so.

Leanness might be selected for if cost of locomotion varies with wing loading. If we assume that wing length correlates with wing area and if for a given wing area fat level correlates with wing loading, then, because fat varied with latitude but wing length did not, southern juncos were more lightly loaded than northern (compare Blem 1975); and their locomotory costs were presumably lower (Pennycuick 1975). Lower mass may also improve agility in flight or accelerate take-offs, both factors
that might increase the probability of escape from predators. We are not the first to suggest that these and other conjectural pressures might be expected to prevail and counterselect against fattening in environments or at times where fat stores are rarely needed (King 1972, Dugan et al. 1981, Freed 1981, Norberg 1981, Stuebe and Ketterson 1982, for birds; Gyug and Millar 1980, Millar 1981, for mammals).

Proximate causes of fattening.—We consider here the results of our multiple regression analysis and what they may reveal about the cues that regulate fat levels and lead to the north–south difference we observed. Studies of seasonal variation in body mass at single locations have often found air temperature to be a correlate of fattening, but the nature of the relationship has varied. Some investigators have observed negative correlations (e.g., Helms and Drury 1960, King and Farner 1966, Blem 1978, King 1972 for summary); others (Haftorn 1976, Biebach 1977), corelations that shift from negative to positive, or vice versa; and still others (Evans 1969), no correlation at all. In our study, even though low air temperature just prior to sampling was associated with greater mass (and high temperature with lesser mass) when effects of other variables were controlled for, air temperature nevertheless accounted for only a very small part of the observed variation. As for other possible cues, day length (Evans 1969, Knowles 1972, Evans and Smith 1975), snow cover (Haftorn 1976, Vincent and Bédard 1976), and wind speed (Dugan et al. 1981) have been found to be significant correlates of fat levels. Evans (1969) reported that day length on the day 30 days before the one on which fat stores of Yellow Buntings (Emberiza citrinella) were measured correlated highly with fat levels, suggesting a proximate cue whose effect, nevertheless, was not immediate. For juncos, we found significant partial correlations between mass and day length and mass and snow cover but, as with temperature, these variables account for very little variation. Evans’ finding may suggest that day length, not at the time of sampling but at some earlier time, might explain some of our unaccounted-for variation (see below).

While we recognize that variables found significant in a regression analysis may not be meaningful to the animals under study, the correlations between mass and snowfall and mass and temperature indicate to us that juncos have some limited capacity to respond to short-term weather changes and, other things being equal, that they increase food consumption or decrease energy expenditures when recent temperatures have been cold and snow is on the ground. If this is correct, the ability to augment and deplete fat stores in response to conditions that vary unpredictably and frequently suggests that juncos are highly sensitive to both the advantages and disadvantages of transporting stored fat.

Why did latitude account for most of the explained variation in body
mass? We attribute this to the high correlation in the eastern United States between latitude and long-term environmental conditions influencing thermoregulatory demands and food availability. Among these conditions are mean December-February air temperature, the lowest temperature ever recorded, mean annual snowfall, and mean daily minimum air temperature in January (Ketterson and Nolan 1976). When physiological or behavioral events of temperate-zone organisms correlate better with long-term means than with current weather, day length is often proposed as the proximate cue that controls those events (Evans 1969, Vincent and Bédard 1976). If, in fact, juncos fatten to a greater degree in the north because days are shorter there than in the south, we must credit them with the ability to perceive and respond to relatively small differences in length of day. At our sampling site in Michigan the shortest day is 9 h 17 min long, as against 9 h 51 min in Alabama (Nautical Almanac, 1981). Alternatively, it may be that juncos cannot discriminate between day-length differences of this magnitude, but rather that the birds themselves differ from place to place, such that northern juncos respond to days of given lengths by fattening to a greater extent than do southern birds exposed to the same cue. A difference in response to an identical cue would imply genetic differentiation among winter populations; it would also imply some association between the mechanism that controls fattening and the mechanism that controls distance migrated. The absence of geographic size (wing length) clines within sex-age classes is circumstantial evidence that members of any particular breeding population scatter widely in winter, i.e., that winter populations are a mix of breeding populations and not likely to be genetically differentiated from north to south. This question obviously deserves further study (Ketterson and Nolan 1982).

Finally, day length need not be the controlling regulatory variable. Northern birds are exposed earlier in the winter season to conditions that elevate metabolism and they, like some mammals (Selander 1952), may respond to cold (after some delay) by an increase in appetite. The fact that juncos everywhere tended to be heavier in late winter could be explained by supposing a summation effect, with northern juncos experiencing some critical weather variable(s) over a longer period or at a greater intensity than southern juncos.

SUMMARY

Many temperate-zone bird species accumulate fat stores during winter. These stores are commonly assumed to serve as energy reserves for the longer nights, colder temperatures, and increased probability of fasting during periods of snow cover; but little is known about what regulates fat storage at the proximate level. If seasonal fattening is a response to winter climate, then a latitudinal cline in degree of fattening would be expected in many parts of the world.
This paper reports such latitudinal variation in the body mass of Dark-eyed Juncos (*Junco hyemalis*) captured at six locations under a variety of environmental conditions during several winters. Juncos at higher latitudes (Michigan and Indiana) were significantly heavier than those from more southern sites (Tennessee, South Carolina, Alabama, and Mississippi). This was true of young and adult individuals of both sexes and was not a function of latitudinal variation in body size (as measured by wing length). Visible fat stores were also greater at higher latitudes, and we conclude that northern juncos were fatter than their southern counterparts.

Multiple regression of body mass on measures of temperature, day length, and snow cover as well as on wing length, latitude, and hour of day indicates that latitude was by far the best predictor of mass; but all the variables produced significant partial regression coefficients. Thus, juncos were heavier when recent temperatures had been colder, when days were longer, and when snow was present. Additionally, they were heavier if they had longer wings or were caught later in the day.

Two explanations of latitudinal variation in fattening are considered. Northern and southern juncos may represent genetically differentiated populations varying in their regulatory physiology. Alternatively, juncos may simply respond in a graded manner to conditions that vary in their proximate physical environments. Results to date can be taken to support either view.

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DEPT. BIOLOGY, INDIANA UNIV., BLOOMINGTON, INDIANA 47405. ACCEPTED 24 AUG. 1983.
VARIATION AND MIGRATION OVERLAP IN FLIGHT FEATHER MOLT OF THE ROSE-BREASTED GROSBEAK

PETER F. CANNELL, JEFFREY D. CHERRY, AND KENNETH C. PARKES

Variation in body plumage of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) has been frequently noted (e.g., Stone 1899, Bagg and Eliot 1937, Whittles 1938, Smith 1966). Variability of flight feather pattern and molt has, to our knowledge, been addressed only twice. Oberholser (1974: 97), incorrectly, and Dwight (1900:97) each commented on the variability of the first prealternate tail molt. In this paper we document variation in the molt and pattern of flight feathers of male Rose-breasted Grosbeaks. We present five cases of arrested wing molt, amplify Dwight's (1900) comments on tail molt, and show that this species differs from the majority of migratory birds by initiating autumn migration while flight feather molt is still underway.

METHODS

We used mist-netted birds and museum specimens to assess the molts and plumages of male Rose-breasted Grosbeaks. Females were omitted from the study for practical reasons; it is difficult to detect feathers of differing ages among their uniformly brown flight feathers.

The mist-netted birds were primarily from Kent Island, New Brunswick, where Cannell and Cherry operated a banding station from July to mid-October 1980. Specimens at the following museums were examined: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), Museum of Comparative Zoology (MCZ), Field Museum of Natural History (FM), New York State Museum (NYSM), and the Buffalo Museum of Science (BMS). Included were collections salvaged from television transmission towers, providing data on birds known to be migrating at the time of death. Specimens salvaged from the towers of WFMJ (Youngstown, Mahoning Co., Ohio), WIC (Pittsburgh, Allegheny Co., Pennsylvania), and WKZO (Gun Lake, Barry Co., Michigan) are at the CM. Birds salvaged from the towers of WGR and WKBW (Buffalo, Erie Co., New York) are at the BMS.

All birds, live and preserved, were examined for molt in a manner similar to that prescribed by Snow (1967). Molt of body plumage was classified as slight, medium, or extensive. Birds molting flight feathers received a score for each flight feather according to the age or stage of growth of that feather.

RESULTS AND DISCUSSION

Arrested molt.—On 28 September 1980, at Kent Island, New Brunswick, Cannell and Cherry mist-netted a second-year male Rose-breasted Grosbeak with symmetrically arrested wing molt. The primaries, tertials, all coverts, and the first (distal) two secondaries were typical black definitive basic (adult) feathers. The third, fourth, fifth and sixth secondaries on
each wing were retained juvenal feathers, brown and worn. There was no active body or flight feather molt. Apparently the molt sequence had been discontinued at this stage, not to be resumed, qualifying as arrested molt, in the sense of King (1972). This last grosbeak of a field season that extended through 13 October was banded, photographed, and released.

A second case of arrested wing molt was found at the MCZ. A second-year male (MCZ 297059) collected on 20 August 1874 at Upton, Oxford Co., Maine, had retained the sixth juvenal secondary on the right wing.

Three additional cases of arrested molt were found among Buffalo tower killed birds. These were after-second-year birds retaining definitive remiges from the previous year’s plumages. Although both of these feather generations are black, the retained remiges show a clear shade contrast with the new remiges, and their terminal white spots are worn away. These birds were salvaged on 21 September 1977 (BMS 7562), 24 September 1970 (uncatalogued), and 29 September 1982 (BMS 7561). None were in active molt, except for the 1982 bird, which had nearly full grown outer primaries. These specimens had retained, respectively, secondaries 4–6, 3–6, and 3–6.

**Arrested and omissive prealternate tail molt.**—Oberholser (1974:858) incorrectly stated that the tail acquired by the “partial prenuptial” (=first prealternate) molt of first-year males is “entirely or in part brown like that of females.” Unlike most birds, Rose-breasted Grosbeaks do renew their tail in the first prealternate molt, but the color of the new generation of rectrices is black. Oberholser may have observed a phenomenon which Dwight (1900:97) understood and described more accurately: this first renewal of tail feathers may be incomplete, with one or more brown juvenal rectrices being retained.

We examined museum specimens to determine the nature and extent of the incomplete spring tail molt mentioned by Dwight (1900). We found it to be surprisingly common. Of 46 males in first alternate plumage in the AMNH, 17 (37%) showed incomplete molt of the tail. Of 22 males in first alternate plumage in the CM, 11 (50%) had failed to molt some rectrices. Of 22 first alternate plumage males in the FM, 15 (61%) showed incomplete tail molt. Comparable frequencies of incomplete tail molt were found among specimens in the MCZ and the NYSM. None of these birds showed active tail molt.

The replacement of rectrices in these birds shows two patterns. In some specimens, replacement is basically symmetrical and sequential, usually with only the central pair, or central two pairs of rectrices having been replaced. Exceptionally (FM 311878) as many as five right and four left rectrices are black adult-type rectrices. These represent cases of arrested molt, in which molt of the feather tract has ceased prior to completion. In
Table 1

Examples of Omissive First Alternate Rose-breasted Grosbeak Rectrices

<table>
<thead>
<tr>
<th>Mus. no.</th>
<th>State/Province</th>
<th>Date</th>
<th>Left</th>
<th>Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH 513966</td>
<td>Ontario</td>
<td>10 May 1889</td>
<td>AAAA</td>
<td>AJ JAA*</td>
</tr>
<tr>
<td>AMNH 56646</td>
<td>Ohio</td>
<td>8 May 1870</td>
<td>AAAA</td>
<td>AAAAAA</td>
</tr>
<tr>
<td>AMNH 53098</td>
<td>Minnesota</td>
<td>13 May 1889</td>
<td>J J J AA</td>
<td>A JJ JA</td>
</tr>
<tr>
<td>AMNH 65920</td>
<td>New York</td>
<td>4 May 1888</td>
<td>JAAAA</td>
<td>AAAAAA</td>
</tr>
<tr>
<td>AMNH 68365</td>
<td>New York</td>
<td>11 May 1890</td>
<td>AAAAAJ</td>
<td>AAAAAA</td>
</tr>
<tr>
<td>AMNH 229771</td>
<td>New York</td>
<td>26 May 1908</td>
<td>A JJ J J</td>
<td>J JJ J J</td>
</tr>
<tr>
<td>AMNH 364719</td>
<td>New York</td>
<td>17 May 1890</td>
<td>A JJ J JA</td>
<td>A JJ J J</td>
</tr>
<tr>
<td>CM 149687</td>
<td>Pennsylvania</td>
<td>17 May 1973</td>
<td>AA J J A</td>
<td>A JJ J A</td>
</tr>
<tr>
<td>CM 151731</td>
<td>Ontario</td>
<td>? May 1900</td>
<td>J JJ J JA</td>
<td>A JJ J A</td>
</tr>
</tbody>
</table>

* J = juvenile rectrix; A = adult rectrix.

other specimens, the location of retained juvenal rectrices is irregular and asymmetrical (Table 1). In these, molt apparently continues to conclusion along the tract, but skipping one or more feathers along the way. We call this phenomenon “omissive molt.”

Dwight (1900) suggested that the prealternate tail molt takes place in “late winter.” This statement is supported and refined by a number of second-year museum specimens with tail feathers in sheath. Two March specimens from Colombia, AMNH 122691 and CM 41722, indicate symmetrical, and sequential tail molt. CM 28091, taken 10 March in Costa Rica, had already completed its entire tail molt and was just completing its body molt. FM 220605, taken in Colombia on 28 February 1950, had just dropped its central rectrices.

Another Colombian specimen (CM 58814), taken 30 November, had replaced the central pair of rectrices (one with traces of sheathing at the base) but was also growing the three outermost right rectrices. That this was not replacement of accidentally lost feathers is indicated by the fact that body molt was also being initiated in a number of tracts on the specimen, and that the three right outer rectrices (R) were growing in normal sequence, not simultaneously (R4 almost full length; R5 about 10 mm; R6 just showing). This specimen would appear to document a case of omissive molt occurring during the first prealternate molt, which therefore may take place early as well as late in the winter.

Prealternate flight feather molt in Rose-breasted Grosbeaks is thought to be restricted to the tails of young birds, entering their first alternate plumage (Dwight 1900). An adult (black-plumaged) male (FM 15799) taken
on 26 March 1904 in Nicaragua showing symmetrical molt of both rectrices and remiges is therefore surprising. It was growing its right and left seventh primaries, and its two left central and three right central rectrices.

Plumage color irregularities.—Dwight (1900) also commented, in regard to the first prealternate tail, that the color might be "deficient." Color deficiency in these rectrices seems to take the form of feathers that shade from solid black to brown, usually within the last centimeter of the tip of the feather. Several skins (e.g., AMNH 364686, 364936; CM 64632) show this tendency.

An adult male (CM 151738) taken in Taunton, Bristol Co., Massachusetts, on 12 May 1916 has a left central rectrix conspicuously browner than the rest. It is no more worn than the other rectrices, so cannot have been retained from a previous plumage. This single brown rectrix may be attributable to a defect in the feather follicle itself, as feathers growing from injured areas in birds are sometimes deficient in pigment (K. Parkes, pers. obs.).

A color variability not mentioned by Dwight (1900) is the tendency toward definitive black coloration in normally brown juvenile remiges (e.g., AMNH 364696, 513969, 53097, and CM flat skin T–164). Such wings show large (up to 25 mm) areas of black on the outer primaries, fading distally to the brown of typical juvenile remiges. The typical "white area at the base of the primaries" described by Dwight (1900:208) for the juvenile plumage may be enlarged to as much as 15 mm, approximating the definitive adult condition. A possibly related observation was made by Cannell, who mist-netted a female Rose-breasted Grosbeak on 17 May 1982 at Fire Island, Suffolk Co., New York, which had one black male-type rectrix (left central) among normal brown female rectrices.

Clearly, the molts and plumages of male Rose-breasted Grosbeaks are more variable than those of other passerine species, at least as these are currently described. The degree of variability in females, in which differences between age classes are inconspicuous and molt irregularities are not so easily noticed, has not been fully studied. Although Dwight (1900) suggested that the prealternate molt of females is limited or non-existent, differing degrees of rectrix wear among spring female specimens from the United States suggests the possibility of an incomplete prealternate tail molt like that of males.

Molt in migrating birds.—A third aspect of the molt of Rose-breasted Grosbeaks, in addition to sequence and coloration, also appears to be unusual. As a rule, migratory species in the temperate zone show little overlap between molt and migration. In most cases migration does not begin, or progress very far, until completion of flight feather molt. Certain species may delay the entire molt until after arrival on the wintering
grounds. Still other species may begin the molt, suspend it for the duration of the migratory journey, and resume it after arrival on the wintering grounds (e.g., certain Sterninae, Columbidae, Nectarinidae, etc.; Snow 1967). This is the "interrupted molt" of Payne (1972) and the "suspended molt" of Prater et al. (1977). In the words of Payne (1972:139), "the temporal separation of molt, breeding, and migration in the annual cycle is often interpreted as an adaptation that minimizes the day-to-day strain on the energy resources of a bird." Unfortunately, subsequent discussion of this topic, by Payne and others, is confined to the energetic relationships of molt and breeding, not molt and migration.

One of the difficulties in addressing the latter topic is the paucity of information on the molt of birds that are actually migrating. The disappearance of birds from a breeding population under study does not necessarily mean initiation of migration. Nor are birds collected at localities intermediate to the breeding and wintering grounds and shown to be undergoing active molt necessarily migrating. In both cases an unknown period of resting, feeding, and local wandering may be occurring. It is nevertheless interesting, in light of information presented below, that two of four adult Rose-breasted Grosbeaks mist-netted at Kent Island, New Brunswick, by Cannell and Cherry during autumn 1980, were molting flight feathers. A third showed arrested molt, as described above.

Birds killed at night by striking some obstacle provide a unique record of birds actually in the process of migrating, but of numerous papers on tower killed birds few report in detail on the status of molt in salvaged specimens. Tordoff and Mengel (1956) comment on molt in tower-killed birds and mention the Rose-breasted Grosbeak as a species that "evidently migrates at times in extensive molt." Two specimens are mentioned: an immature in heavy body molt and an adult male in both body molt and heavy flight feather molt.

We examined specimens salvaged from five television transmission towers, described above. These samples included over 4000 autumn-killed passerine birds, including 57 adult male and female Rose-breasted Grosbeaks. Of these, 52 (91%) showed active wing molt, usually including both primaries and secondaries. Five specimens show active tail molt. Most of these, as well as all specimens of immature Rose-breasted Grosbeaks, also show body molt. Of the specimens showing wing molt, 33 have either only the outermost (P9) or only the two outermost (P8, P9) pairs of primaries sheathed at the base. Only three specimens show primaries other than these in molt. One of these (CM 150648) has P2 and P3 about \( \frac{3}{4} \) grown on the right wing, but completed on the left. The other two have P7 more than half grown. In the 16 specimens that were not molting primaries, a varying number of secondaries were growing. The most ex-
treme example, a female (CM 150651), has left S2 growing, with S3 and S4 not yet shed; on the right wing, S3 is growing, and S4, S5, and S6 are not yet shed.

One of the Michigan wings (CM T–3676) apparently shows an omissive molt pattern. In this specimen, P9 and S4 are not yet full grown, S5 is a retained worn juvenal feather, and S6 and all other remiges are new. It is impossible to know whether S5 might have been renewed later, out of sequence, or retained until the next complete prebasic molt the following autumn. In the latter case, the molt would be classified as omissive.

Although it is impossible to know the source of the grosbeaks that struck the TV towers, it is clear that in at least part of its range this species initiates its autumn migration well before completion of the prebasic molt. Some birds that hit the towers would have been growing feathers for several days thereafter, at the least.

An examination of the rest of the large samples confirms that overlap of molt and migration is exceptional. Most of the species represented were vireos and wood warblers with lesser numbers of Gray Catbirds (*Dumetella carolinensis*) and thrushes (*Hylocichla mustelina* and *Catharus* spp.). Most of these showed no molt whatsoever. Only the Red-eyed Vireo (*Vireo olivaceus*) showed a high proportion of adult birds with flight feather molt (8 of 26 examined). Further details of these samples will be presented in another paper.

**SUMMARY**

Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) are extremely variable in several aspects of their flight feather molt. They have a high frequency of arrested molt of the remiges. They commonly show arrested and “omissive” molt in the prealternate rectrix molt of the first-year males, of which as many as half may replace only part of the tail. The coloring of adult and juvenal feathers shows great variability. Finally, most Rose-breasted Grosbeaks that strike TV towers during their nocturnal migration in the autumn are still molting flight feathers. No other species studied thus far shows such a prevalence of active molt during migration.

The reasons for variability in molt and plumage are unknown, as are the reasons for an apparent relative lack of variability in the molt and plumage of other species. We hope that this paper will prompt further investigation of molt variation, and of overlap between molt and migration, in Rose-breasted Grosbeaks and other species.

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Youngstown, Ohio, for organizing the salvage projects at WFMJ; to several individuals, including J. Matviya and R. Mulvihill, for salvaging specimens at WIIC, and to C. Fichtel for his meticulous documentation of molt, cranial, and other data during his preparation of hundreds of specimens. R. Adams of the Kalamazoo (Michigan) Nature Center kindly donated the specimens salvaged at WKZO. This is contribution number 52 of the Kent Island Scientific Station, Kent Island, New Brunswick.

LITERATURE CITED


ORNITHOLOGY DEPT., AMERICAN MUSEUM OF NATURAL HISTORY, 79TH STREET AND CENTRAL PARK WEST, NEW YORK, NEW YORK 10024; DEPT. BIOLOGICAL SCIENCES, STATE UNIV. NEW YORK, ALBANY, NEW YORK 12222; AND CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE, PITTSBURGH, PENNSYLVANIA 15213. ACCEPTED 25 APR. 1983.
GENERAL NOTES

Autumnal Zugunruhe and migratory fattening of Dark-eyed Juncos apparently suppressed by detention at the wintering site.—Study of Zugunruhe, as a basis for determining the existence and intensity of the underlying physiological state of migrants, has established the importance both of internal factors such as circannual rhythms and of external environmental factors such as photoperiod in inducing and suppressing the migratory condition (Gwinner, pp. 391–410 in Aschoff, Biological Rhythms. Plenum Press, New York, New York, 1981). Other external factors that have been investigated are characteristics of the migratory destination (Wagner and Schildmacher, Vogelzug 8:18–19, 1937; Sauer and Sauer, Vogelwarte 20:4–31, 1959; Gwinner, J. Orn. 109:70–95, 1968; Gwinner and Czeschlik, Oikos 30:364–372, 1978). Transport of individuals in autumn to the winter range of the species (Gwinner 1968) or in spring to the breeding range (Emlen, Auk 84:309–342, 1967) has not suppressed Zugunruhe, nor has exposure of newly arrived migrants captured at their own individual destinations and held there had that effect in spring (Merkel, Z. Tierpsychol. 13: 278–301, 1956; Gwinner and Czeschlik 1978). However, interpretation of spring experiments is difficult because physiological changes associated with reproduction may be involved in terminating the vernal migratory state (Gwinner and Czeschlik 1978).

We asked whether detaining migratory Dark-eyed Juncos (Junco hyemalis hyemalis) outdoors during the breeding season at a location in which they had wintered in previous years would inhibit normal Zugunruhe and migratory fattening the following autumn. This detention (at Bloomington, Monroe Co., Indiana, 39°N, 87°W) exposed the birds in the weeks preceding the normal migration season to the environment of the precise location to which they would have migrated, had they summered on their northern breeding range. If the birds recognized the site as their goal, possibly their migratory physiology would be affected, although the absence of effect would not necessarily indicate non-recognition. Our findings suggest that characteristics of the migratory destination can terminate, or perhaps even prevent initiation of, the migratory state, at least in autumn.

The migratory eastern junco.—Migratory members of J. h. hyemalis in eastern North America move between a summer range located largely in Canada and a winter range covering nearly the entire eastern United States. Fall migrants probably begin to leave the breeding range in August, and winter populations build up until about 1 December, when migration ceases (Ketterson and Nolan, Ecology 57:679–693, 1976). Probably throughout the winter range, spring migration begins about 1 March; some juncos are found in the northern reaches of the winter range until mid-May. Sex and age classes differ in distance migrated: females travel farther than males, on the average, and adults tend to winter south of young hatched during the preceding breeding season (Ketterson and Nolan 1976; Auk 96:532–536, 1979; Auk 99:243–259, 1982; Current Ornith. 1:357–402, 1983).

Adult male juncos are faithful to their previous breeding sites, adult females less so (Ketter-son and Nolan 1983; pers. obs.). Our investigations of winter populations at five latitudes (33°N–42°N) have shown that some males and females return every winter to the same few hectares (Ketterson and Nolan 1982). Once it has shown site fidelity, a junco probably returns to that site every winter until it dies; we base this conclusion on high annual rates of return (53%) after the first expression of winter site fidelity (Ketterson and Nolan 1982). Thus, a junco that in the future would be faithful to its winter site can be identified by its having returned in the winter following that in which it was banded.

Juncos hatched during the preceding breeding season can be aged until about 31 December by inspection of skull pneumatization. Birds in their second winter cannot be distinguished
from older birds. Determination of sex by external characters is reliable (Ketterson and Nolan 1976).

Methods.—We divided juncos into three groups, which differed in their previous histories but not in experimental treatment. Experiments were done in autumn 1980 and spring 1981. Except during experiments, groups were intermingled in large outdoor cages (e.g., about 7 \times 4 \times 3 \text{ m}). Group histories before the experiments were as follows.

Group I (two males and two females): All had wintered at least twice at Bloomington before the experiment. Three were banded during the winter of 1978–79 and immediately released; the fourth was banded in 1976, released, and caught again at the same place in the following winters. All were captured in 1979–80 at their original capture sites, three near the aviary cages in which we subsequently held them and the fourth 1.5 km from the aviary. Thus, from last recapture until the experiment began in September 1980, at least three of the four could see surroundings long familiar to them. The breeding locations of Group I birds were unknown.

Group II (one male and one female): The female, adult when caught on 1 August 1979 at Timmins, Cochrane Co., Ontario, Canada (49°N, 81°W), and the male, immature when caught on 3 September 1979 at Wawa, Algoma Co., Ontario (49°N, 85°W), were transported within 2–3 days approximately 1250 km southward to Bloomington and caged. Therefore, Group II was like Group I in that its members had no experience on the breeding range during the spring and summer preceding the autumn experiment. Group II differed from Group I in that the Group II birds had been transported into the winter range instead of having been caught there: the immature male had never migrated and had never been on the breeding grounds as an adult. Probably the most important difference between Group I and Group II members is that the sites to which Group II would have migrated in autumn were unknown. The probability that Group II juncos would have settled at or even passed through Bloomington is negligible given the extensive winter range of migratory juncos.

Group III (eight males and eight females in the autumn experiment, three of the same males and six of the same females in the spring experiment): We caught these as breeding adults in late July 1980 at Wawa, took them immediately to Bloomington, and caged them with the other groups. All could have been as old as or older than the members of Group I and Group II, and some probably were (see below). All had spent at least one winter living free before capture; and, as with Group II, very likely none had ever wintered at or passed through Bloomington.

On 3 September, members of groups were randomly assigned to individual steel-wire cages (21 \times 27 \times 20 \text{ cm}) on the roof of a five-story building 1.5 km from the outdoor aviary. The birds were visually isolated but could hear each other. Transparent plexiglass covers sheltered cages from rain, and during severe precipitation larger sheets of plywood were set on top of the plexiglass. All birds could see a segment of sky whose north–south angle was about 160° and whose east–west angle was about 100°. The segment seen varied slightly from cage to cage, and most birds were moved occasionally from one cage to another. We observed no changes in behavior or physical condition as a result of shifting birds to different cages.

Dim light reached the roof from windows of a building about 100 m distant, but the juncos could not see these windows. A calibrated Tektronix J6511 photometer with its illuminance probe directed upward from the roof floor at the midpoint of the layout of cages recorded lux values (x of five readings) of 0.050 on cloudy nights, 0.229 on half-moonlit nights, and 0.267 on full-moonlit nights.

The geomagnetic fields within the aviary cages differed little or not at all from the normal local field; but from one experimental (registration) cage to another the horizontal angle of a compass needle varied by as much as 100°, apparently because of variation in the proximity
of girders and a nearby machine room and, perhaps, differences in remnant magnetism among the cages.

Each cage's perch was attached to a microswitch connected to an Esterline-Angus event recorder. Every use of the perch was recorded on a strip chart moving at 30.5 cm/h. We tallied 30-sec intervals during which a cage's perch was activated at least once and then counted the number of such intervals among the 900, 30-sec intervals that fall between 21:00 and 04:30. We selected these hours because they encompassed the period of darkness on the longest days of both autumn and spring. The number of an individual's active 30-sec intervals is its nightly Zugunruhe “score.” We found for each individual its seasonal score (sum of nightly scores), maximum nightly score, and number of nights it was active for at least 30 min (i.e., nightly score ≥60). We also computed medians of the nightly scores according to group.

Compilation of all nightly scores in autumn 1980 revealed that scores from two nights per week were sufficient for the purposes of this paper. Therefore, we analyzed and present data from only two nights per week in both the autumn and spring experiments; single scored nights were separated by two, three, two, three, etc., un-scored nights. A total of 33 nights were scored in the autumn experiment (7 September–26 December), 28 nights in the spring experiment (26 February–31 May).
Because the sexes were equally represented in each autumn group, we have simplified the presentation by pooling results from the sexes. Occasional gaps in the nightly record for individual cages were caused by equipment failures and by exercise periods (see below). To reduce the effect of these on total seasonal scores, we arbitrarily assigned to a missing score the mean of the individual's score on the two nights preceding and two nights following the gap. In spring 1981, a Group I female escaped when five scoring nights remained before the experiment ended. Because Group I was small, data for this female are nevertheless used and are presented without extrapolating to scores for the missing nights.

Four birds at a time were taken separately in opaque bags to exercise in the outdoor aviary for 2 or 3 days in early or mid-November. There the large cages were divided into individual compartments (about 3.5 × 2.0 × 3.0 m), each covered by cloth so that its occupant could see no other experimental bird but could see the sky and surroundings in two directions. In spring 1981 there was no interruption for exercise.

Weights (to 0.1 g on a 50-g Pesola balance) and subcutaneous fat classes (0–5 with zero low, as described by Helms and Drury [Bird-Banding 31:1–40, 1960], and Nolan and Ketterson [Wilson Bull. 95:603–620, 1983]) were determined in mid-afternoon at the beginning and end of both experiments and also at approximately 2-week intervals during experiments. Autumn weights are analyzed only for the values recorded through 1 December because the tendency of juncos to fatten in winter could confound interpretation of December weights. (In fact, December weight changes were small or absent.) Male juncos average larger than females. However, because we present means of absolute individual gains and of gains as a percentage
of initial weight, for each group we pooled data without regard to sex. Increases in weight were accompanied by increases in fat class, and we believe that the weight gains observed were largely the result of fattening (see Nolan and Ketterson [1983], for the correspondence between winter weights and fat class).

Results.—In the autumn experiment the birds of Group I were much less restless than were members of the other two groups, which among themselves were indistinguishable in their Zugunruhe. Fig. 1A shows the nightly medians of each group and reveals how greatly Group I differed from the others in this respect. Table 1 presents for each group its median score and the lowest and highest score of its members for the three measures of Zugunruhe. It also gives, for each measure, the ranks of the scores of group members when all 22 birds were pooled and ranked, lowest to highest. In a Mann-Whitney U-test, Groups II and III did not differ in any measure. For seasonal score, \( U = 11, 2\)-tailed \( P > 0.10 \); for maximum nightly score, \( U = 13, 2\)-tailed \( P > 0.10 \); for nights scored above 60, \( U = 13, 2\)-tailed \( P > 0.10 \). Accordingly, we pooled Groups II and III and tested them against Group I. For seasonal score, \( U = 1, 2\)-tailed \( P = 0.002 \); for maximum nightly score, \( U = 3, 2\)-tailed \( P < 0.002 \); for nights scored above 60, \( U = 0, 2\)-tailed \( P < 0.002 \).

Mean autumn weight gain by members of each group is shown in Table 2. Group I birds gained much less than did members of the other two groups, which did not differ among themselves. As in Zugunruhe, Groups II and III were combined because they were similar (absolute gain, \( U = 15.5, 2\)-tailed \( P > 0.10 \); percentage gain, \( U = 13, 2\)-tailed \( P > 0.10 \)). Group I differed significantly from Groups II–III (absolute gain, \( U = 4.5, 2\)-tailed \( P < 0.02 \); percentage gain, \( U = 6, 2\)-tailed \( P < 0.02 \)). Fat classes at time of maximum weight for Group

---

**Table 1**

**Zugunruhe Scores in Autumn 1980 and Spring 1981, According to Group**

<table>
<thead>
<tr>
<th>Season and group</th>
<th>Median (extremes) ranks(^a)</th>
<th>Seasonal score</th>
<th>Maximum nightly score</th>
<th>Nights scored &gt;60</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group I</td>
<td></td>
<td>310 (187, 1137)</td>
<td>122 (55, 465)</td>
<td>2 (0, 4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1, 2, 3, 5</td>
<td>1, 2, 3, 7</td>
<td>1, 2, 3, 4</td>
</tr>
<tr>
<td>Group II</td>
<td></td>
<td>5502 (3760, 14,243)</td>
<td>598 (508, 688)</td>
<td>17.5 (17, 18)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7, 15</td>
<td>9, 17</td>
<td>6.5, 8</td>
</tr>
<tr>
<td>Group III</td>
<td></td>
<td>6511 (1023, 13,366)</td>
<td>604 (247, 828)</td>
<td>22.5 (6, 29)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>all others</td>
<td>all others</td>
<td>all others</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group I</td>
<td></td>
<td>7840 (2533, 12,478)</td>
<td>753 (567, 877)</td>
<td>14 (8, 17)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2, 6, 7, 15</td>
<td>2, 3.5, 9, 15</td>
<td>1, 4.5, 4.5</td>
</tr>
<tr>
<td>Group II</td>
<td></td>
<td>10,054 (9500, 10,609)</td>
<td>804 (778, 830)</td>
<td>20 (18, 22)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10, 12</td>
<td>8, 13</td>
<td>6, 12</td>
</tr>
<tr>
<td>Group III</td>
<td></td>
<td>9113 (1705, 11,926)</td>
<td>766 (230, 837)</td>
<td>20 (9, 24)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>all others</td>
<td>all others</td>
<td>all others</td>
</tr>
</tbody>
</table>

\(^a\) See text for methods.

\(^b\) The number of junco ranked was 22 in autumn, 15 in spring.
I birds were 0, 1, 1, 2. Only one of the Groups II–III juncos was classed as 1, and the median rank was 4.

In spring, Zugunruhe of all juncos was greater than in fall, and the intergroup differences that had existed in autumn disappeared (Fig. 1B and Table 1). As before, we compared Group I juncos to Groups II and III combined, using Mann-Whitney tests of ranks: for seasonal score, $U = 21$, 2-tailed $P > 0.10$; for maximum nightly score, $U = 17.5$, 2-tailed $P > 0.10$; for number of nights scored above 60, $U = 4$, 2-tailed $P > 0.05$. In this last comparison the female that escaped before the end of the experiment is excluded. The trend toward fewer nights with activity in Group I can be seen in Fig. 1B: Group I birds did not become active until about 1 April, when their Zugunruhe set in rather synchronously and thereafter remained high.

In spring weight and fattening, Group I birds became as heavy as, or heavier than, the other juncos (Table 2). For absolute gain and percentage gain, $U = 13$ and 8, respectively, 2-tailed $P > 0.05$. Fat classes at the time of maximum weight for Group I birds were 4, 4, 4, 5. Both Group II birds were classed as 5, and the median class of the Group III birds was 3.5.

Discussion.—Our samples were small, but we very cautiously suggest that the site-faithful juncos did not enter the normal autumn state because they were already at the place to which they would have migrated had they been free. Other factors that might have sup-

<table>
<thead>
<tr>
<th>Season and group</th>
<th>Mean (extremes) ranks</th>
<th>Gain as % of initial weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Absolute gain (g)</td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group I</td>
<td>2.15 (0.5, 2.9)</td>
<td>12.0 (0, 18)</td>
</tr>
<tr>
<td></td>
<td>1.3, 4.5, 6.5</td>
<td>1.3, 5, 7</td>
</tr>
<tr>
<td>Group II</td>
<td>4.90 (4.0, 5.8)</td>
<td>24.5 (21, 28)</td>
</tr>
<tr>
<td></td>
<td>9.5, 16</td>
<td>10, 14</td>
</tr>
<tr>
<td>Group III</td>
<td>5.14 (2.0, 8.5)</td>
<td>28.6 (10, 52)</td>
</tr>
<tr>
<td></td>
<td>all others</td>
<td>all others</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group I</td>
<td>6.00 (5.1, 6.8)</td>
<td>32.9 (29, 35)</td>
</tr>
<tr>
<td></td>
<td>8, 9, 11, 13</td>
<td>9, 11, 12, 14</td>
</tr>
<tr>
<td>Group II</td>
<td>6.35 (6.0, 6.7)</td>
<td>29.0 (25, 33)</td>
</tr>
<tr>
<td></td>
<td>11, 12</td>
<td>8, 10</td>
</tr>
<tr>
<td>Group III</td>
<td>3.98 (1.1, 7.1)</td>
<td>20.8 (6, 47)</td>
</tr>
<tr>
<td></td>
<td>all others</td>
<td>all others</td>
</tr>
</tbody>
</table>

a In autumn, means of initial and of maximum absolute weights (g) by sex for each group were: for Group I males 18.8, 20.6, for females 17.5, 20.0; for the Group II male 18.8, 22.8, for the female 20.7, 26.5; for Group III males 19.4, 24.0, for females 17.1, 22.8. In spring, means of initial and maximum absolute weights (g) by sex for each group were: for Group I males 18.3, 24.6, for females 18.0, 23.6; for the Group II male 20.3, 27.0, for the female 23.9, 29.9; for Group III males 21.1, 25.0, for females 18.6, 21.9.

b The number of juncos ranked was 22 in autumn, 15 in spring.

c The percentage gain of each individual was determined from its initial and maximum weights; percentages were summed within groups, and means per group were derived from sums.
pressed the migratory state, but that we tentatively reject, are advanced age and long captivity, possibly coupled with group living, and/or exposure to a pre-migratory photoperiodic regime unlike that of the breeding range. Although older juncos sometimes show less autumn Zugunruhe than young of the year (Swanson, M.A. thesis, San Jose State Univ., San Jose, California, 1976), age seems to us an unlikely explanation for our results because at the time of the autumn experiment all members of each group would have been making at least their second autumn migration. Group I subjects would have been making at least their third; but given the junco’s 53% annual survival rate (Ketterson and Nolan 1982, 1983), probably at least half the Group III subjects would have been doing the same. Captivity of Group I at Bloomington and the fact that they shared aviary cages with 15–20 other juncos at the time when Group III juncos were breeding could account for the difference between those two groups, but Group II was held with Group I and nevertheless fattened and grew restless. Group II subjects had, in fact, been held 4–6 months longer than Group I; yet in all measures of Zugunruhe both Group II members ranked higher than all Group I members (1-tailed P = 0.067, the lowest possible value for samples of two and four). Daylength during summer is considerably shorter at Bloomington than at Wawa (1 h 40 min shorter on the longest day). Recent work by Moore et al. (Condor 84:410–419, 1982) suggests that in White-crowned Sparrows (Zonotrichia leucophrys gambelii) the normal expression of the annual phase of the annual cycle requires exposure to 16-h days. The longest day at Bloomington is 15 h 58 min, and this might have suppressed Zugunruhe and fattening in the Group I juncos. Here again, however, members of Group II also experienced these shorter days and despite that were more like Group III than like Group I.

If recognition of some feature(s) of the winter site did have the suggested effect, what might the feature(s) have been? The local geomagnetic field of Bloomington is a possibility. The birds were exposed to this force until the experiment began; thereafter, however, they experienced disturbed fields that varied from cage to cage. Visual cues characteristic of the latitude and longitude of the winter range have been thought (Wagner and Schildmacher 1937) to influence Zugunruhe. More specifically, Sauer and Sauer (1959) reported that sight of the starry African sky suppressed restlessness in members of four Syl
dia species displaced to their winter quarters (and beyond) in Africa. An obvious difficulty with applying this suggestion to our Group I results is that the stars (except Polaris) at Bloomington in the weeks preceding the autumn experiment, i.e., in the period in which suppression of the migratory condition supposedly occurred, were in different positions from their positions in winter. Therefore, the juncos, if they looked at the stars, did not see the familiar sky of their winter site. A final familiar feature to which the Group I juncos were exposed was the landscape. Three individuals in at least two winters had home ranges around the aviary cages in which they spent the summer before the experiment. The fourth had been caught and recaught 1.5 km distant, but nevertheless could have known the aviary grounds; occasionally banded individuals have moved back and forth between the aviary and the station where this fourth bird was caught.

The suggestion that familiar surroundings inhibited the migratory condition in Group I is not inconsistent with the notion that an endogenous circannual rhythm or that photoperiod regulates migration in juncos. Even in his early report of circannual rhythms in Phylloscopus spp., Gwinner (1968) emphasized that although displacement to the winter range of the species had not suppressed Zugunruhe, displacement to the individual’s precise winter quarters might cause suppression. To relate our autumn experiment to Gwinner’s, our Groups II and III roughly correspond in treatment and in results to his Group III; but our Group I had no counterpart in his experiment.

Acknowledgements.—We are grateful for the assistance of many Indiana University students and especially to Miki Stuebe, Mike Shelton, Ann Burke, and Jim Vincent. Thomas S. H.
Mimicry of the human voice by European Starlings: the role of social interaction.—Although vocal mimicry by European Starlings (Sturnus vulgaris) has often been noted (e.g., Bent, U.S. Natl. Mus. Bull. No. 197, 1950), the development of it has never been formally studied. The present report describes social constraints on starling mimicry and suggests possible functions. Although the targets of the mimicry here were humans, the major aim of the study was to understand how starlings naturally select sounds for mimicry. In other words, is their mimicry a faithful imitation of their social or physical surrounding or is it, as in most other species, quite biased toward a particular class of sounds? Because humans can detect speech more acutely than avian sounds, speech mimicry was used as an analogue to natural starling mimicry. As the presence of speech could be easily perceived, it would thus be possible to identify the origins of any mimicked sounds, as well as conditions under which starlings mimic their social world.

Methods and materials.—Seven starlings, four females and three males, were captured as five-day-old nestlings (Table 1). They were hand reared in the laboratory by the investigators until approximately 30 days of age. During this period, they were maintained as a group with equivalent and extensive contact with human caretakers. At day 30, a male and a female were assigned to the interactive contact (IC) condition, a male and female to the limited contact (LC) condition, and the remaining three to the auditory contact (AC) condition. IC1 and IC2 each remained in the homes of the respective investigator who had reared them. Each received daily vocal attention and companionship from its human caregiver. In addition, each had a male Brown-headed Cowbird (Molothrus ater) housed with it in a 0.7 × 1.3 × 1.3-m hardware-cloth cage. Explicit attempts to "teach" IC1 and IC2 speech were avoided, i.e., food or social contact was not offered as a reward for mimicry although each of these items was clearly sought by the birds. Whistled songs (e.g., "Dixie," "Popeye the Sailorman") were performed daily, usually when the birds were allowed to fly free and interact with their human caretakers. Mimicry by IC1 and IC2 was often imitated by the humans but again only in an unsystematic manner, i.e., the humans did not consciously imitate sounds as a particular strategy. Finally, IC1 and IC2 were exposed to tape-recorded passages of human speech and whistled songs twice daily for one month.

The LC starlings were also housed in homes, but with different caregivers who had not participated in the starlings' care as nestlings. Each bird was also housed with a cowbird companion. Because these birds were less "tame" with their new human caregivers, they were rarely allowed to fly free or to contact humans directly. Each was housed, however, in a room allowing it extensive vocal stimulation from humans. That is, they heard speech in their environment but were not "spoken to" consistently or allowed interaction with humans. The LC birds were not tutored by tape recordings. The AC birds were housed as a group in a cage (4.8 × 4.8 × 3.2 m) on a screened porch belonging to one of the investigators where they could hear all of the interactions inside the home where IC2 was housed. As a result, the auditory environment of the AC birds was yoked to the IC condition. Thus, they were
also exposed to the tape-recorded speech and songs twice daily for a month. Although these birds were originally as tame as the others, they quickly became quite shy with humans in that they both ceased to solicit food from humans and avoided being handled by humans.

All seven birds were fed an identical diet based on the Bronx Zoo diet for omnivorous birds and were given fresh water with vitamins and fresh food daily. Although IC and LC birds also received occasional “snacks” (e.g., fruit or cheese) from their caregivers, the amount of food obtained in this manner was insufficient to be of dietary consequence and was composed of food items already abundantly present in their normal mash. Thus, all the birds had identical exposure to humans until day 30 and then differed subsequently in terms of the social quality of their contact with human caregivers.

All the birds were tape-recorded regularly, producing about 1 h of vocalizations for each bird each week for 4 months. The birds were recorded at different times of the day across this period using an Uher 4200 Report recorder and an Uher 517 microphone.

The tapes resulting from these sessions were then transcribed and the birds’ vocalizations were classified into five categories: clear human speech, human-produced sounds (e.g., whistling and indistinct speech), non-conspecific avian vocalizations, mechanical noises, and starling vocalizations. Random passages of tapes from all the birds were coded by a second observer. Observer agreement was high (89%), with the most disagreement involving distinguishing clear speech and speech-like sounds. All transcriptions of clear speech were also analyzed for content to ascertain the human origin of the mimicry.

Results.—Both starlings in the IC condition mimicked human sounds extensively. For IC1, 49% of his mimicry derived from human speech and another 25% from human whistling. Likewise, IC2’s percentage of human mimicry was 68%, 28% comprising speech and 40% whistled tunes. For each bird, however, the proportion of mimicked speech that was highly articulate was low, 9% for IC1 and 4% for IC2. This figure derives from use of very strict coding criteria and the high degree of articulation and intelligibility required on the starlings’ part to be clearly understood on audiotape. Using the broader criterion of speech-like sounds seems a fairer procedure in that human speech when spoken by humans into tape recorders may not be clearly intelligible but is unmistakably identifiable as human speech. This was the case for the starlings as well.

None of the LC or AC birds ever mimicked human speech although they all mimicked mechanical noises and other birds, most notably the cowbird companions of the LC birds (Table 1). Here their mimicry was frequent and quite accurate, reproducing even some of the higher frequency components of cowbird song (around 9 kHz). This frequency range exceeds that published for the starling voice; previous studies had recorded a maximum of only 8.2 kHz (Brand, Auk 55:263–268, 1938). Finally, no bird ever mimicked the tape-recorded passages although IC1 did mimic the mechanical noise of tape hiss.

Origin of the mimicry.—For both IC1 and IC2 the major part of their human mimicry could be attributed to sounds produced by their human caregivers. This was evident not only by content but by their distinct mimicry of the male caregivers’ intonation patterns. It was, in fact, clear to other listeners whom the birds were mimicking. In both cases, the birds rarely mimicked the female spouses of their investigators although the spouses had frequently interacted with the birds after capture. In terms of content, the selectivity of their mimicry was also evident. IC1 mimicked speech patterns such as “Good morning, Rex [IC1’s name]” and statements such as “it’s time,” “Basic research” and “Hi.” The latter vocalization he subsequently used in interactions with humans and with other birds. IC2 frequently said her name as well as often repeated statements such as “You’re a crazy bird.” Both birds were prolific, if off-key, whistlers and produced mimicked whistled songs of several seconds duration that were clearly recognizable. Most often, whistled tunes, easily recognized as distinct to humans, were combined by the starlings, e.g., IC1 would whistle a few
Table 1
A Summary of the Experimental Conditions and Results for Starling Mimicry

<table>
<thead>
<tr>
<th></th>
<th>Interactive contact</th>
<th>Limited contact (LC)</th>
<th>Auditory contact (AC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subjects</td>
<td>one male and one</td>
<td>one male and one</td>
<td>two females and one</td>
</tr>
<tr>
<td></td>
<td>female, individually housed with a male cowbird</td>
<td>female, individually housed with a male cowbird</td>
<td>male, housed together</td>
</tr>
<tr>
<td>Experience</td>
<td>daily human companionship and 1 month of tutoring by tape recording</td>
<td>routine care from humans and exposure to human conversation</td>
<td>routine care from humans, 1 month of individual tutoring by tape recording; exposure to human speech of IC2 but limited visual contact</td>
</tr>
</tbody>
</table>

Content of mimicry

<table>
<thead>
<tr>
<th></th>
<th>Interactive contact</th>
<th>Limited contact (LC)</th>
<th>Auditory contact (AC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Speech sounds</td>
<td>39%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Whistling</td>
<td>33%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Mechanical noises</td>
<td>5%</td>
<td>1%</td>
<td>0%</td>
</tr>
<tr>
<td>Avian sounds</td>
<td>16%</td>
<td>49%</td>
<td>3%</td>
</tr>
<tr>
<td>Starling sounds</td>
<td>7%</td>
<td>50%</td>
<td>97%</td>
</tr>
</tbody>
</table>

Notes of “Dixie” followed by several notes of “Swanee River.” The whistled tunes also appeared to go through many idiosyncratic variations that were solely created and re-created by the starlings. Another interesting feature of their mimicry was their combination of sounds that naturally occurred together, such as an episode consistently mimicked by IC1 comprising the sounds of a door opening and dogs barking, followed by saying “Good morning, Rex,” and the production of a whistled tune used by his caregiver as a greeting. This was in fact the daily scenario as the caregivers’ dogs were let outside, followed by IC1 being released from his cage and given his customary greeting.

Analysis of the recording sessions also revealed the repetitions quality of the mimicry, especially of the companion cowbird’s song or of whistled tunes that would be repeated “verbatim” hundreds of times in rapid succession. For example, IC1 once mimicked the cowbird’s song 256 times in succession during one 30-min session.

Sonograms of mimicry by IC1 appear in Fig. 1. Because the aim of the study was not to determine how accurately starlings could mimic speech, but to learn under what conditions they could produce recognizable speech, no extensive efforts were made to obtain high quality tape recordings for acoustic analysis. Thus, the sonograms may underestimate the starlings’ mimicking accuracy. We judged the quality of mimicry by listening to audio tapes rather than by visual inspection of sonagrams. The actual content of the mimetic sequences was easily determined with this method in the same way that human speech is perceptible and articulate to listeners when heard over the telephone even though much acoustic detail is missing. That such detail is also lacking in starling “speech” is demonstrated by the sonagrams. The question of the absolute accuracy of the starling’s mimicry awaits further analysis.
Fig. 1. Transcriptions of the mimicry by ICI: “Mere, Rex, c’mere, Rex, c’mon” by human and starling, respectively, with a narrow band setting; same content with a wide band setting; starling and speech-like sounds by starling; speech-like sounds by starling; “Hi” by starling and human, respectively, with a narrow band setting; same content with wide band setting (the first sound for the starling is his mimicking of a human sniffing followed by “Hi”); starling mimicry of a cowbird song; cowbird song by a cowbird. Sonograms were made on a Kay 6061B SonaGraph.

Several exemplars of the starling’s mimicry are shown in Fig. 1. The phrase, “Mere, Rex, c’mere Rex, c’mon,” was exceptionally distinct to listeners, particularly its intonational patterns which accurately imitated the cajoling sound of the speaker. This utterance was used frequently by humans to get ICI back into his cage, a sometimes frustrating task. The word “Hi” is also shown. This word was also used extensively by ICI, especially during contact with humans, which was, of course, the context in which the word was also experienced by ICI.
The category of "speech-like sounds" represented a fascinating array of vocalizations characterized mostly by mimicry of the cadence of human conversation, i.e., the characteristic intonation contours marking statements or questions. To listeners, it sounded like a person talking in a muffled voice. A transcribed version of a sequence such as that shown in Fig. 1 would read as follows: "because effects," 'such rules became effects,' whistle, starling sound, 'just because effects'". (It should be noted that neither ICl or IC2 had ever had extensive experience with conspecific vocalizations as they were hand-reared and removed from contact with other starlings at 30 days of age.) The best human analogue to the starlings' speech-like sounds is the expressive jargon of human infants (Dale, Language Development: Structure and Function, Holt, Rinehart and Winston, New York, New York, 1976). In the early stages of language development, infants produce conversation-like speech with the appropriate intonation although the words are either not clear or are poorly produced. Moreover, as is characteristic of the repertoires of infants (Lenneberg, Biological Foundations of Language, Wiley & Sons, New York, New York, 1967), many of the stock phrases present in the starlings' jargon were often-repeated phrases that typically occurred at the beginning or end of utterances.

A final important quality of the starlings' mimicry of speech was that they also imitated the act of speaking, i.e., the physical sounds of smacking lips and breath inhalation that accompanies speech. Their mimicry thus included the broad vocal context of speaking, not just the linguistic or perceptual event of speech. A related example of this is shown in Fig. 1 where each of IC1's imitations of "Hi" is preceded by a sound unmistakable on tape as a human sniffing. The origin of this combination was most likely the chronic respiratory infection of his caregiver who suffered from allergies to birds.

Discussion.---The data show the selectivity of starling mimicry and its dependence upon the nature of the social interaction between the starling and its mimicked partner. As in duetting or mimicry by other species (Todt, Z. Tierpsychol. 39:178–188, 1975), starling mimicry may function to define particular social relationships. Social relationships formed at an early age may be the most important for determining mimicry. We have subsequently taken IC2 and housed her with a different caregiver who periodically attempted to socialize with her by offering food; she has adopted new, but limited, forms of mimicry. Reinstatement of the type of social interaction present for a young nestling, e.g., dependence upon another for food, and perception of the caregiver as a "surrogate" companion, may facilitate the formation of such social bonds (Hartshorne, Georgia Oriole 26:23–27, 1961).

In any case, we offer these data as empirical evidence of the environmental origins of starling mimicry. Clearly what is important to the starling is the nature of the social relationship with its mimicked partner: only when humans served as actual interactants were they the target of mimicry. Likewise, when cowbirds or starlings filled this role, as in the LC and AC conditions, they constituted the starling's mimicry. Perhaps a function for starling mimicry in large flocks is that their mimicry serves as "passwords." As such, the data are consistent with past work done on other starlings (Bertram, Anim. Behav. Monogr. 3:79–192, 1979) as well as in other social avian species (Payne, Anim. Behav. 29:688–697, 1981; Feekes, Z. Tierpsychol. 58:119–152, 1982).

A final note—in order to distinguish this work from those in which birds, most recently the African Grey Parrot (Psittacus erithacus), have also been "taught" to talk (Todt 1975; Pepperberg, Z. Tierpsychol. 66:139–160, 1981). Although our method for transmitting human speech is consistent with the highly social quality of the tutoring methods used by Todt (1975) or Pepperberg (1981), and may in fact rest on similar social principles, our starlings were never consciously trained or taught any particular word or phrase. All speech was used as a method of social interaction modelled after how humans use speech with each other, particularly how adults use speech with children. Our aim was to see if social companionship with auditory exposure and no explicit training would be
enough to produce mimicry. It was. What the outcome of explicit training procedures would be with starlings remains to be explored. We offer these data as an incentive for others to pursue the study of these talented and companionable birds.

Acknowledgments.—Funding was provided by grants from Sigma Xi and the National Science Foundation (BNS 78-07223). We thank David Eastzer and Gayle Stroud for help in obtaining and rearing the birds; W. G. Hall and J. E. R. and Nada Staddon for serving as “foster” homes; and Luis F. Baptista and Edward H. Miller for their careful reviews of the manuscript.—MEREDITH J. WEST, A. NEIL STROUD, Dept. Psychology, Univ. North Carolina at Chapel Hill, Chapel Hill, North Carolina 27514, and ANDREW P. KING, Dept. Psychology, Duke Univ., Durham, North Carolina 27706. Accepted 15 Mar. 1983.


Study area and methods.—Songs of breeding Black-throated Gray Warblers were recorded during April and May of 1981 and 1982 near the west entrance of the Finley National Wildlife Refuge (FINLEY), Benton Co., Oregon, using a Nagra III recorder and Gibson parabolic microphone, model P-200. The study area (about 30 ha) was characterized by a mixture of mature Oregon white oak (Quercus garryana) and Douglas-fir (Pseudotsuga menziesii). A more complete description of the study area, including a description of the habitat use and foraging behavior of black-throated grays at FINLEY, was given by Morrison (Auk 99:503–513, 1982). About eight male black-throated grays were located in the study area each year. The songs of at least five different individuals were recorded in 1981; we do not know if songs recorded in 1982 were of the same or different individuals as those in 1981. Songs recorded in the wild were analyzed on a Kay Elemetrics Sona-Graph Model 7029A using the 300 Hz wide band filter and the 80–8000 Hz frequency spectrum. The resulting sonagrams were studied to compare song types recorded at FINLEY. All tape recordings made in this study were deposited in the Florida State Museum Bioacoustic Archives as FSM master tape numbers 560, 563, and 577. About 50 h on 20 days for the 2 years of study was spent recording and observing the singing behavior of the black-throated gray. About 70% of the observations were conducted within 3 h of sunrise; 15% were conducted during late morning and 15% during afternoon. About 80% of the fieldwork was conducted in 1981.

Tapes used for playback experiments were made by transferring the original recordings to cassette tapes; experiments were also conducted using the Nagra and the original tapes.
Experiments were conducted by placing a speaker within 30 m of a singing, and thus likely territorial, male black-throated gray; a description of these experiments is presented elsewhere (Morrison 1982).

Terminology used to describe the function of song types herein conforms to that presented elsewhere: our type-I song corresponds to the “accented ending song” and type-I song, and our type-II song corresponds to the “unaccented ending song” and type-II song as summarized by Kroodsma (1981).

Results.—Two distinct types of songs, plus a modification of one song type, were identified during this study. Type-II songs are 1.3–1.5 sec long, begin softly, and with each figure increase in amplitude, forming a crescendo (Fig. 1A). Each motif up to the last one consists of two rapid frequency modulated figures. The first of these figures is the lower pitched, centering in the first four motifs at 3.9–4.2 kHz, and in the fifth one at about 4.8 kHz. To the ear and eye it is a buzzy, only slightly tonal sound. (Its tonal character is evident when the sound is played at half speed, and it then may be described as a guttural warble.) The second figure of each motif is the higher pitched one, ranging from about 4.2–5.8 kHz in the first four motifs to 4.5–6.3 kHz in the fifth, which is the penultimate figure of the entire song phrase. These second figures of the motif are less rapidly modulated. They still sound buzzy, but the rising and falling tonality can be heard and seen. The final motif of the song is composed of a single lower-pitched stroke-glissando figure that is a purely tonal whistle, rising abruptly from 4.8–5.5 kHz and then falling to 3.0 kHz. A phonetic rendering of the complete song phrase might be: buzz see buzz see buzz see buzz see wweeo.

Type-I songs are more complex and difficult to describe or render phonetically. The simpler type-I’s are about 1.3 sec long and consist of three guttural warbles in which the warble
motifs have several up-down glissandos so rapidly uttered that they run together (Fig. 1B). These are followed by a series of three less guttural and discretely separated up-down glissando warble figures and a terminal figure composed of a buzz leading into a short stroke steep glissando ending. The frequency span of the song is mostly from 3.0–5.2 kHz until the last motif, which rises to 4.0–6.8 kHz. Phonetically it might be rendered: wurtelee wurtelee wurtelee wurtelee wurtelee wurtelee buzzeoz.

The more complex type-I’s are about 1.5 sec long (Fig. 1C). They have an opening motif of five or six rapid guttural warbles in which three stroke-gllissandos form a vibrato at 3.0–5.8 kHz. This is followed by a broad buzz centered at 4.0 kHz, then a higher guttural buzz, an up-down glissando, and a buzzy rising-then-falling whistle. Phonetically it might be written: wurtelee wurtelee wurtelee wurtelee wurtelee buz buzz wurtelee buz; but phonetics are not applied easily or aptly to such a complicated utterance.

The final song, the “soft song,” is apparently not a distinct song type. Soft songs were given by males closely attending females and are type-II songs uttered at low amplitude (Fig. 1D). This difference in amplitude is not a factor that can be shown readily in a sonogram. At least in the one shown (Fig. 1D) the pitch starts out at the same frequency as normal type-II songs, but ends at 6.5–7.0 kHz.

Black-throated grays are already singing upon arrival at FINLEY in mid-April. Observations of females (e.g., carrying nesting material) indicated that most nest-building was completed by the first week of May. Individual birds were not followed for continuous periods of time; therefore, the exact proportion of time that different song types were sung was difficult to quantify. Prior to 1 May, we estimated that type-II song was given for 95% of 25 h of observation. Beginning about 1 May, the frequency of type-II decreased and the use of type-I increased. As the study area was not visited on consecutive days, the change from type-II to type-I could only be approximated: during 25 h of observation in May and early June, the use of type-I increased until both song types were used equally. Although only short visits were made to the study area during late June and early July, it appeared that type-I was the most frequently used song type during this latter stage of nesting. Although it was difficult to follow individual birds for more than a few minutes, both type-I and type-II songs were given both from exposed perches (e.g., treetops) and while foraging (i.e., within the canopy).

The final song, called the “soft song,” was sung only when males were seen closely following their (apparent) mate while the female was gathering nesting material or foraging. This song could not be heard by the human ear more than about 10 m away from the singer.

When either type-I or type-II songs of the black-throated gray were re-played to a singing conspecific, the bird responded only with type-II song regardless of whether the bird was singing type-I or type-II prior to playback. Birds responded to playback by approaching to within a few meters of the speaker; results for these experiments were presented elsewhere (Morrison 1982).

Males were also observed at least 10 occasions (undisturbed by playback) to switch from type-I to type-II when one approached to within apparently close (for the black-throated gray) proximity of another male (i.e., 20–30 m). Approaches of under 30 m usually resulted in the chasing of one bird by the other.

Discussion.—Type-II song in the Black-throated Gray Warbler apparently functions in territory establishment and defense and mate attraction, during early stages of the breeding period. This conclusion is supported by results of playback experiments—males always responded with type-II regardless of the song type presented. The frequency of type-II decreased after territory boundaries had become fixed and nesting was well underway.

The “soft song” apparently functions in male and female communication when birds are in close proximity. We do not know if the information content in this song differs from that
of the typical type-II, or if it is simply the result of male nervousness (or anxiety) because of the closeness of the female.

The use of type-I song is more difficult to explain. Morse (1966, 1967) concluded that type-I (his type B) functioned in courtship and pair-bond maintenance with the female in several eastern *Dendroica* warblers: this has been criticized by others (see later). Kroodsma (1981) also suggested that type-I and type-II songs of the *Dendroica* warblers he studied could be related to mate selection and territorial defense, respectively. We doubt, however, that the specific function of type-I in the black-throated gray is male-female solicitation. Remember that type-I was not given during the early stages of the breeding period; thus it is not likely that type-I is reserved specifically for courtship. An additional hypothesis, concerning the function of multiple song types, was given by Krebs (1977, 1978) (see also McGregor et al., Am. Nat. 118:149–151, 1981; Yasukawa, Anim. Behav. 29:114–125, 1981). Krebs reasoned (the “Beau Geste” hypothesis) that repertoires allowed a territorial male to create the impression that there were several birds in his territory; new arrivals would thus falsely believe that there was a higher density of conspecifics in the area and thus settle elsewhere. Application of Krebs’ hypothesis to our results seems inappropriate. If black-throated grays sought to create a false impression about density at FINLEY, then both type-I and type-II should be used during and shortly after arrival, and not after nesting is initiated.

We believe a more parsimonious explanation for the song types of the black-throated gray has already been given. Using the Black-throated Green Warbler (*D. virens*) studied by Morse (1967) as a model, Lein (1972, see also 1978) suggested that the black-throated green will normally produce type-I. But the addition of various external stimuli during the breeding period, such as the presence of a conspecific male, will cause a “frenzied” response which stimulates type-II (his type A) song. Absence of stimuli for type-II (and the “soft song”) will automatically result in the production of type-I. Singing behavior of the black-throated gray can thus be viewed as a variation of a continuum. Both type-I and type-II song thus carry the same general information; that is, proclamation of identity.

Acknowledgments.—Data analyzed herein were collected in part while the senior author was a Research Assistant in the Oregon Cooperative Wildlife Research Unit; I thank numerous individuals at Oregon State Univ. for fruitful discussions concerning the contents of this paper. I am especially grateful for reviews by D. E. Kroodsma and D. J. Martin; although responsibility for ideas presented herein remains with the authors, their suggestions greatly improved the quality of this paper. Lori Merkle is thanked for typing several drafts.—MICHAEL L. MORRISON, Dept. Forestry and Resource Management, Univ. California, Berkeley, California 94720, and JOHN WILLIAM HARDY, Florida State Museum, Univ. Florida, Gainesville, Florida 32611. Accepted 28 Apr. 1983.


**Song response by female Red-winged Blackbirds to male song.**—Several studies have demonstrated that information may be transmitted within the temporal components of songs of birds (Falls, Proc. XII Int. Ornithol. Congr. 259–271, 1963; Emlen, Behaviour 41: 130–171, 1972; Thorpe, Behaviour Suppl. 18, 1972). While investigating the role of female vocalizations in the Red-winged Blackbird (*Agelaius phoeniceus*) social system, Corral noticed that, during the early part of their breeding season, female red-wings often gave their songs immediately following the songs of their mates. Whenever this response occurred, the females either initiated their songs within approximately 1 sec of male song, or midway through the song of the male. Examples of these timing relationships are presented in Fig. 1d–f. During the spring of 1978 Corral observed the singing behavior of mated pairs of red-
wings with the objective of determining if this male-female vocal interaction was temporally and biologically significant.

**Methods.**—Observations were conducted on a field in Old Field, Long Island, New York. Male red-wings, polygynous breeders, arrive in spring several weeks before females. Females arrived in mid-April in 1978 and subdivided the larger male territories into smaller, female "sub-territories" (Nero, Wilson Bull. 68:129-150, 1956; pers. obs.), which were defended from conspecific females. Males in the present study had one to three females nesting on their territories. The boundaries of the male territories and female sub-territories were determined by noting song perches and then connecting the outermost of these points. Birds were not marked, but spectrographic analysis of male song recordings made throughout the breeding season showed that all four males observed on the field maintained the same territories for the duration of the study (Smith et al., Condor 82:259-266, 1980). In addition, several banding studies have shown that female red-wings tend to maintain territorial position during the breeding season (Nero, Wilson Bull. 68:5-37, 1956; Lenington, Anim. Behav. 28: 347-361, 1980; three of four females banded by M. Hayes at the University of Michigan/Dearborn Biological Field Station in 1981 remained on their territories).

Female red-wings sing two distinct song types (Fig. 1a, b). At times the two song types are combined into a single song, usually consisting of type 1 song figures followed by type 2 figures. Type 1 song appears to function in pair-bond maintenance, while type 2 appears to be an aggressive vocalization, sung chiefly in the presence of territorial intruders (Beletsky,
The average percent response of female song to male song during the breeding season. Percent response = no. of female responses/no. of male songs given. The numbers inside the histogram bars are the number of pairs of red-wings, out of the possible seven, observed on each day.

Z. Tierpsychol. 62:47–54, 1983). The differential use of the two song types was not documented in 1978, but it was obvious that, although type 2 song occasionally followed male song, type 1 was sung by the females in the great majority of these situations. For a description of male red-wing song, see Orians and Christman (Univ. Calif. Publ. Zool. 84, 1968) or Smith et al. (1980).

Observations took place between 06:00 and 08:00 EST on the dates appearing in Fig. 2. The frequency and time of occurrence of male and female songs were recorded verbally into a cassette recorder, yielding a real-time record of the acoustic activities of the birds. Observations were begun when mated individuals were within 5 m of each other and ended when one of the birds flew out of sight (usually 5–10 min). Though only a fraction of the red-wing pairs were observed on any one day, over the 17 observation days all pair combinations were observed (two males had one female each on their territories, one had two females, and one had three females = seven possible pair combinations). From field observations and
playback experiments of male song to resident females performed in 1977, it was determined
that a 1-sec-response criterion would closely reflect the natural timing of female songs to
male song, i.e., a female was considered to have responded to a specific male song if her
song followed the termination of that song within 1 sec. The percent response of a female
to mate song was determined by dividing the number of female song responses by the total
number of male songs sung during the observation period.

Recordings were made with a Nagra IV-L tape recorder through a Sennheiser 211 micro-
phone mounted on a 46 cm parabolic reflector. Sonagrams were prepared using a Kay Ele-
metrics Vibralyzer model 7030A using the 300 Hz filter.

Results.—The first females arrived on the male territories on 17 April. On 21 April, when
observations were initiated, all seven females were present on the territories. The data
presented in Fig. 2 indicate that females consistently sang over 30% of their songs in response
to male song within days of their arrival on territories of males; this high rate, averaging
over 65% during some observation days, was maintained by the females under observation
through most of May. As male and female red-wings typically sing at rates of four to five
songs/min (Smith. Behaviour 56:136—156, 1976) and three songs/min (Beletsky, Anim. Behav.
31:355—362, 1983), respectively, and mean song durations for both sexes routinely fall be-
tween 1.0 and 1.5 sec (Smith et al. 1980; Beletsky 1983), the high percentages of male
songs responded to vocally by females clearly depart from percentages that would be ex-
pected if chance alone was temporally connecting the songs. After 20 May, percent response
to male song declined; this decrease coincided with an increase in the occurrence of copu-
latory and nest-building behaviors.

Discussion.—Data presented in Fig. 2 support the idea that female red-wings often respond
immediately to their mates’ songs with their own songs. The females of several other icterine
species have been observed to answer their mates’ songs with their own vocalizations, in-
cluding Common Grackles (Quiscalus quiscula) (Wiley, Z. Tierpsychol. 40:244—264, 1976),
Western Meadowlarks (Sturnella neglecta) (Falls, pp. 61—89 in Advances in the Study of
Northern Orioles (Icterus galbula) (Beletsky, Condor 84:445—447, 1982) and Brown-headed
Cowbirds (Molothrus ater) (Dufy, Anim. Behav. 30:1043—1052, 1982).

Corral noted that females did not appear to sing in response to non-mate (neighbor and
intruder males) song. However, playback experiments reported on elsewhere (Beletsky and
Corral, J. Field Ornithol. 54:200—202, 1983) indicated that female red-wings responded with
song to playback of both mate and non-mate male song. It was concluded that females re-
sponded vocally to any male occupying the territory: in the natural course of events, the
male occupying the territory is the mate.

It is possible that one function of female song and its timing to male song is to convey
pair-bond status information to the mate. Thorpe (Nature 197:774—776, 1963) suggested that
songbird duets, precisely timed mutual singing between mates, may maintain or strengthen
the pair-bond, facilitate the synchronization of reproductive physiologies, and keep mates
aware of each other’s locations. Evidence that red-wings use temporal information in their
vocal communication system is given by Smith and Norman (Condor 81:83—84, 1979) who
report “leader-follower” singing in male red-wings. They found that resident males sang
their songs immediately following intruder songs at a relatively invariant time interval. It
was proposed that this acoustic interaction served to signal to the intruding males that the
resident male was responding directly to the intruder. Likewise, it is possible that the female,
by timing her song to that of the male, is conveying to her mate information such as her
individual identity, physiological state and/or other pair-bond information. Since the response
of females to male song is seemingly restricted to the pre-nesting phase of the breeding cycle,
some aspect of the female song response could indicate to the male the female’s readiness
to breed. Two advantages that might accrue to the female by singing in this relationship to her mate are: (1) most of the information is likely to be received by the male at a time when he is silent; and (2) constant repetition of the message at a fixed time interval would more clearly inform the male that the female is responding directly to him.

The results of this preliminary study indicate that at times the female red-wing is timing her song to follow her mate’s song. Although more work is needed to describe the content of the information being exchanged, the mode of information exchange described now in inter- and intra-sexual social contexts for Red-winged Blackbirds might present a common, but usually overlooked form of animal communication.


The purpose of this study was to examine in detail characteristics of song perches used by four species of passerines that breed in sagebrush-grassland habitats; Brewer’s Sparrow (Spizella brewerti), Vesper Sparrow (Pooecetes gramineus), Western Meadowlark (Sturnella neglecta), and Horned Lark (Eremophila alpestris). My objectives were: (1) to describe vegetational features of song perches used by each species; (2) to make interspecific comparisons; and (3) to determine if there were preferences in use of perches compared to what was available. Several questions were addressed. Do individuals tend to select relatively large and conspicuous perches from which to sing? Do individuals that occupy the same local area show species-specific patterns of use? How do perches differ among vegetationally different sites? Are available perches limiting to shrubland and grassland birds?

Study area and methods.—The study was conducted 20 April–18 June 1980 on three 16-ha sites on the Vernon Division of the Wasatch National Forest, 10 km S of Vernon, Tooele Co., Utah. This cold desert area is located at 1800 m elev. in the southern end of Rush Valley. Big sagebrush (Artemisia tridentata) dominated two sites; one that had been plowed and seeded to grasses in 1963 (NONMAN) and one that had been chained and seeded in 1976 (CHAIN). The remaining site (BURN) was dominated by grasses, but sagebrush islands missed by a controlled burn in 1976 comprised 8% of the site. The most common grasses were bluebunch wheatgrass (Agropyron spicatum), crested wheatgrass (A. cristatum), cheatgrass (Bromus tectorum), and Sandberg bluegrass (Poa sandbergii). More detailed site de-
### Table 1

**Characteristics (± SE) of Randomly Sampled Shrubs**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NONMAN N = 80</td>
</tr>
<tr>
<td>Random shrub height (cm)</td>
<td>43.9 ± 2.1</td>
</tr>
<tr>
<td>Neighboring shrub height (cm)</td>
<td>42.6 ± 2.1</td>
</tr>
<tr>
<td>t</td>
<td>0.54 NS&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Random shrub cover (dm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>18.9 ± 1.8</td>
</tr>
<tr>
<td>Neighboring shrub cover (dm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>18.9 ± 2.2</td>
</tr>
<tr>
<td>t</td>
<td>0.00 NS</td>
</tr>
<tr>
<td>Random shrub volume (dm&lt;sup&gt;3&lt;/sup&gt;)</td>
<td>17.0 ± 2.2</td>
</tr>
<tr>
<td>Neighboring shrub volume (dm&lt;sup&gt;3&lt;/sup&gt;)</td>
<td>17.0 ± 2.5</td>
</tr>
<tr>
<td>t</td>
<td>0.01 NS</td>
</tr>
<tr>
<td>Intershrub distance (cm)</td>
<td>66.6 ± 2.7</td>
</tr>
<tr>
<td>Shrub density (no./30 m&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>22.2 ± 0.8</td>
</tr>
</tbody>
</table>

<sup>a</sup> Stratified sample; burned stratum (N = 83), unburned stratum (N = 23).

<sup>b</sup> Denotes statistical significance (NS P > 0.05; * P < 0.05) of paired t-tests between random and neighboring shrubs.


Singing males were observed primarily in the mornings. When a bird was heard singing, it was located and the song perch measured immediately or marked with flagging and measured at the end of the sampling period. No more than 10 observations were taken on any individual during a sampling period. A minimum of 14 Brewer’s Sparrows and 11 individuals of each of the other species were represented. For each perch, the following measurements were recorded: bird species, shrub species, shrub condition, and height and maximum diameters of shrub crown taken perpendicular to each other and parallel to the ground. The horizontal distance from the center of the song perch to the center of the nearest shrub was recorded and identical shrub measurements taken on the latter.

Shrub density was determined by counting all shrubs in a 30-m<sup>2</sup> circular plot around the song perch. Shrub cover was estimated by calculating the area of an ellipse using shrub diameter values. An estimate of shrub volume was obtained by using height and diameter measurements in the formula for the volume of an ellipsoid. To determine preferences for perch-sites, data were taken on 80 shrubs and their nearest neighbor on both the NONMAN and CHAIN sites along eight randomly located transects stratified to cover all four quadrants of each site. The BURN site was sampled with a stratified random design with 83 points located in the grassland portions and 23 in the sagebrush islands.

Relative availability of shrubs for perches was obtained by weighting the shrub composition of each study site by the number of observations for each bird species sampled on the site. For each study site, a comparison of random shrubs with their nearest neighbor showed no detectable differences in shrub species or shrub condition. Hence, frequencies were com-
bined in calculating available shrub species and condition values. Frequencies of shrubs used by bird species were analyzed using Chi-square or binomial tests (Conover, Practical Nonparametric Statistics, Wiley and Sons, New York, New York, 1971).

Categorical data analysis was used to determine differences among bird species in the proportional use of type and condition of perches. This statistical procedure uses the logarithm of the frequencies for each class of factors (in this case bird species, perch type, and perch condition) to conduct an analysis of variance (ANOVA) using weighted regression (Fienberg, The Analysis of Cross-classified Categorical Data, MIT Press, Cambridge, Massachusetts, 1977). To test for differences in perch variables by species and site, a one-way ANOVA was conducted with 12 treatments (all combinations of four species and three sites). Multiple comparisons in the form of Scheffé’s tests were used to examine differences.

Stepwise discriminant function analysis was used to illustrate differences among bird species with respect to perch preferences. This multivariate statistical method examined the importance of variables for maximally distinguishing between the perch types used by each species. Each of the four perch variables was first transformed to its natural logarithm to satisfy normality assumptions. Perch volume was not included in the discriminant model because the contribution of this variable was nonsignificant (Approximate $F < 1.0$). From formulas in Sokal and Rohlf (Biometry, W.H. Freeman and Company, San Francisco, California, 1969), 99% confidence ellipses were constructed using discriminant scores of the first two functions.

Results.—Virtually all (99.4%) shrubs sampled on NONMAN were sagebrush and 94.4% were living. All shrubs sampled on CHAIN were sagebrush and 83.8% were living. For sagebrush islands on BURN, only sagebrush was found and 95.7% were living. In contrast, only 3.6% of the shrubs in grassland areas of BURN were living and most (97.6%) were sagebrush. Weighting by the respective areas of each stratum, values of availability for BURN were 97.8% sagebrush and 11.0% live shrubs.

Characteristics of shrubs on each site are shown in Table 1. Because shrubs were randomly sampled, differences in size between a shrub and its nearest neighbor were not expected.

### Table 2

<table>
<thead>
<tr>
<th>Perch type</th>
<th>Bird species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BS N = 110</td>
</tr>
<tr>
<td>Shrub</td>
<td></td>
</tr>
<tr>
<td>Big sagebrush (<em>Artemisia tridentata</em>)</td>
<td>93.6</td>
</tr>
<tr>
<td>Utah juniper (<em>Juniperus osteosperma</em>)</td>
<td>5.5</td>
</tr>
<tr>
<td>Utah serviceberry (<em>Amelanchier utahensis</em>)</td>
<td>0.9</td>
</tr>
<tr>
<td>Coralberry (<em>Symphoricarpos orbiculatis</em>)</td>
<td>0.0</td>
</tr>
<tr>
<td>Forb</td>
<td></td>
</tr>
<tr>
<td>Prickly poppy (<em>Argemone corymbosa</em>)</td>
<td>0.0</td>
</tr>
<tr>
<td>Other</td>
<td></td>
</tr>
<tr>
<td>Fence post</td>
<td>0.0</td>
</tr>
<tr>
<td>Fence wire</td>
<td>0.0</td>
</tr>
<tr>
<td>Wooden stake</td>
<td>0.0</td>
</tr>
</tbody>
</table>
A. Shrub Type. Sagebrush □, Other ■

B. Shrub Condition. Alive □, Dead ■

Fig. 1. Shrub type and condition of song perches (P), neighboring shrubs (N), and available shrubs (A) used by four species of sagebrush-grassland birds.
Table 3

PERCH CHARACTERISTICS (\( \bar{t} \pm SE \)) OF SAGEBRUSH-GRASSLAND BIRDS.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Bird species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BS N = 110</td>
</tr>
<tr>
<td>Perch height (cm)</td>
<td>84.9 ± 1.9a</td>
</tr>
<tr>
<td>Neighboring shrub height (cm)</td>
<td>61.4 ± 1.9</td>
</tr>
<tr>
<td>( t )</td>
<td>9.67***</td>
</tr>
<tr>
<td>Perch cover (dm(^2))</td>
<td>61.6 ± 5.2a</td>
</tr>
<tr>
<td>Neighboring shrub cover (dm(^2))</td>
<td>27.3 ± 2.2</td>
</tr>
<tr>
<td>( t )</td>
<td>6.36***</td>
</tr>
<tr>
<td>Perch volume (dm(^3))</td>
<td>95.8 ± 10.5a</td>
</tr>
<tr>
<td>Neighboring shrub volume (dm(^3))</td>
<td>31.8 ± 3.7</td>
</tr>
<tr>
<td>( t )</td>
<td>5.90***</td>
</tr>
<tr>
<td>Intershrub distance (cm)</td>
<td>76.8 ± 7.2a</td>
</tr>
<tr>
<td>Shrub density (no./30 m(^2)])</td>
<td>19.7 ± 0.5a</td>
</tr>
</tbody>
</table>

\(^a\) Dissimilar letters across columns denote nonsignificant differences of perch characteristics between bird species.
\(^b\) Denotes statistical significance (NS P > 0.05; * P < 0.05; *** P < 0.001) of paired \( t \)-tests between perches and neighboring shrubs.
\(^c\) \( N = 104 \) (BS), \( N = 73 \) (VS), \( N = 94 \) (WML), \( N = 64 \) (HL).

unless a bias for encountering larger shrubs existed in the sampling scheme. Paired \( t \)-tests showed no differences between shrub size variables except for greater mean height of neighboring shrubs on the CHAIN site compared to randomly sampled shrubs.

Three hundred and fifty-eight song perches were recorded being used by Brewer’s Sparrows, Vesper Sparrows, Western Meadowlarks, and Horned Larks in this study (Table 2). Shrubs were used 98% of the time. Big sagebrush, the most numerous shrub on each study site, was also the primary song perch used by each species. Perches other than sagebrush (primarily Utah juniper \( Juniperus osteosperma \)), however, were used more frequently than expected based on their availability (Fig. 1A, P vs A). The pattern of use was consistent among all species and highly significant (\( P < 0.001 \)) using binomial tests. This pattern is further substantiated by the fact that perches, compared to the adjacent shrub (Fig. 1A, P vs N), were more likely to be a shrub other than sagebrush. Using Chi-square tests for independence, differences were significant for Vesper Sparrow (\( \chi^2 = 28.32, df = 1, P < 0.001 \)), Western Meadowlark (\( \chi^2 = 26.53, df = 1, P < 0.001 \)) and Horned Lark (\( \chi^2 = 11.10, df = 1, P < 0.001 \)), and Brewer’s Sparrow (\( \chi^2 = 4.66, df = 1, P < 0.05 \)).

In contrast to a consistent preferential use of juniper perches, no apparent patterns of use were detected for the condition of song perches (Fig. 1B). Living perches were preferred by Brewer’s Sparrow (binomial test, \( P < 0.01 \)), but their use by all other species was essentially random (\( P > 0.05 \)). Chi-square tests for independence failed to detect differences between the condition of perches and neighboring shrubs for Brewer’s Sparrow (\( \chi^2 = 0.09, df = 1 \),...
Intershrub Distance  Shrub Density  DF1

Fig. 2. Bird species ordination using 99% confidence ellipses along the first two discriminant functions (DF).

NS), Vesper Sparrow ($\chi^2 = 2.34$, df = 1, NS), Western Meadowlark ($\chi^2 = 0.10$, df = 1, NS) or Horned Lark ($\chi^2 = 0.75$, df = 1, NS).

Categorical data analysis indicated significant differences in the relative use of perches by all bird species pairs except Vesper Sparrow and Horned Lark. Brewer's Sparrows used relatively more living sagebrush for song display, while other species used a greater proportion of juniper perches along a gradient from Western Meadowlarks to Horned Larks to Vesper Sparrows.

Juniper perches averaged 143 cm in height (N = 100) which was significantly greater ($t = 6.37$, df = 102, $P < 0.001$) than the mean height of 80 cm for sagebrush perches (N = 258). Living shrubs had a mean height of 91 cm (N = 231) which did not differ significantly ($t = 1.87$, df = 153, NS) from the mean of 104 cm (N = 112) for dead perches.

Height, cover, and volume are measures of perch size and, for all species, their mean values exceeded those of the nearest neighboring shrub (Table 3). Paired $t$-tests showed these differences to be significant in all cases except two. Due to the large variation in estimates of volume of perches used by Vesper Sparrows and Western Meadowlarks, differences were not significant.

Scheffé's tests revealed differences in the characteristics of perches used by the four bird species (Table 3). Species or site differences were exhibited by perch height ($F = 4.70$; df = 11, 346; $P < 0.001$), intershrub distance ($F = 10.78$; df = 11, 346; $P < 0.001$), and shrub density ($F = 51.69$; df = 11, 323; $P < 0.001$), but not by perch cover ($F = 1.65$; df = 11,
346; NS) or perch volume (F = 1.32; df = 11, 346; NS). Brewer’s Sparrows and Horned Larks both used low perches, but the former species frequented areas of high shrub density while the latter was found in more open areas. Western Meadowlarks used the highest perches and Vesper Sparrow perches had intermediate characteristics. Confidence ellipses derived from discriminant function analysis illustrate the characteristics of the perches used by each species (Fig. 2). Shrub density was the most important variable in discriminating between species followed by perch height and intershrub distance. The characteristics of perches used by Brewer’s Sparrows were more distinctive than those used by other species. Considerable overlap occurred in all species, however, and the discriminant function analysis was unable to classify perches very accurately.

Scheffe’s tests were also used to examine differences in perch characteristics among the three sites. Because birds were not equally common on all sites, sites with few observations were deleted from the analysis (i.e., Brewer’s Sparrow on BURN [N = 4]; Vesper Sparrow on CHAIN [N = 4]; Horned Lark on NONMAN [N = 3]). With some exceptions, each species selected similar-sized perches without regard to site (Table 4). Only Western Meadowlarks used higher perches on NONMAN and BURN compared to CHAIN. Tall junipers were not present on CHAIN unlike the other sites, which may account for this discrepancy. Shrub density and intershrub distance were highly significant for all bird species in contrasts involving the BURN site. These patterns suggest that birds selected similar ranges of perch sizes, but shrub densities and intershrub distances were subject to constraints of the available habitat.

**Discussion.**—These data suggest that for the four species of birds studied, song perches are not used randomly, but show species-specific selectivity as influenced by availability. Three of the four species are considered grassland residents (Kendeigh, Condor 43:165–174, 1941), but Brewer’s Sparrow is sagebrush-dependent (Braun et al., Wilson Bull. 88:165–171, 1976). Hence, the data must be interpreted in light of the habitat preferences of each bird species. In addition, factors other than habitat may be important in the selection of song perches. These include territory size and type, territorial behavior, and body size. Western Meadowlarks had the largest territories, followed by Vesper Sparrows and Brewer’s Sparrows. Territories of Horned Larks were difficult to delineate because birds fed outside defended areas. Birds with large territories would have a wider variety of perches from which to sing

<table>
<thead>
<tr>
<th>Bird species</th>
<th>Site</th>
<th>Variable</th>
<th>Perch height</th>
<th>Perch cover</th>
<th>Perch volume</th>
<th>Intershrub distance</th>
<th>Shrub density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewer’s Sparrow</td>
<td>X</td>
<td>X</td>
<td>NS*</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Vesper Sparrow</td>
<td>X</td>
<td>—</td>
<td>NS*</td>
<td>NS</td>
<td>NS</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Western Meadowlark</td>
<td>X</td>
<td>X</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Horned Lark</td>
<td>—</td>
<td>X</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>***</td>
<td>***</td>
</tr>
</tbody>
</table>

* Denotes statistical significance (NS P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001) of Scheffe’s tests.
given comparable perch densities. Body size may also be a factor because a larger bird would require a stouter perch to support its weight compared to smaller species. Brewer's Sparrows and Vesper Sparrows sing only from elevated perches while Western Meadowlarks and Horned Larks sing during flight and from the ground, the latter to a much greater extent. The conspicuousness of perches and locatability of singing individuals may also be important considerations in selecting a perch in which to engage in territorial song display.

Preferences of birds for juniper perches can best be explained by differences in shrub height. Junipers used as perches were significantly higher than sagebrush perches. No consistent pattern of use was observed between living and dead perches (Fig. 1B), and indeed, living shrubs used as perches did not differ significantly in height from dead perches.

Many authors (Kendeigh 1941; Smith, Wilson Bull. 75:159–165, 1963; Berger, U.S. Natl. Mus. Bull. 237:868–882, 1968; Wiens 1969; Wiens, Ecology 54:877–884, 1973) have noted that selection for high perches occurs, but only Harrison (1977) attempted to test the hypothesis that individuals prefer the highest perches available. Using artificial perches 1.5 and 2.0 m tall, he found that only one (Eastern Meadowlark [Sturnella magna]) of six species observed (Vesper Sparrow was included) showed a statistically significant preference for higher perches. Although the artificial perches stood above the surrounding vegetation and were used extensively by all species, he concluded that individuals will use virtually any elevated perch regardless of height. The lack of demonstrable preferences by birds for higher perches (Harrison 1977) may have been due to the wide spacing of perches (80 m minimum distance). At this low density, territorial birds will have few perches to select and the pattern of perch use probably reflects territory use. My data suggest that if two different-sized perches were placed in close proximity (i.e., 1 m), the higher would be used almost exclusively. In 91% of the instances in the present study, the perch selected by an individual was as high as or higher than the adjacent shrub. Smith (1963) found that Grasshopper Sparrows (Ammodramus savannarum) abandoned low perches if higher ones were provided.

Nonsignificant differences in perch heights between sites (Table 4) indicate: (1) that sites were similar in vegetation structure; (2) that birds frequented similar microhabitats on each site; or (3) that birds selected similar perches on each site. All were true in certain cases. Bird species using different sites frequented similar habitats and perched on similar-sized shrubs. The CHAIN site was unique in that it lacked the conspicuous junipers favored by Western Meadowlarks. Thus, significant site differences in perch height were comparisons of CHAIN with other sites. No significant height differences were detected in the cases of Brewer’s Sparrow and Horned Larks because few territories of these species contained large junipers. However, these birds may not readily use perches exceeding some unknown maximum height.

Factors other than height may play a role in the selection of perches. Utah juniper is a stout shrub and offers good support for perching. Western Meadowlarks, the largest of the birds studied, used Utah juniper more frequently than all other shrubs except sagebrush, and Brewer’s Sparrows, the smallest bird, used Utah juniper least frequently. Nonwoody plants were generally not used as song perches suggesting that physical support of an individual is important in selecting perches. Grass stalks were widely available as perches and are used extensively by birds in grassland areas lacking shrubs (Wiens 1969). Dead shrubs offer more support for perching because smaller twigs break off and leave more large diameter twigs compared to living shrubs.

Species patterns in use of perches appear to indicate that partitioning of available perches may be occurring. My observations, however, do not support this hypothesis. Means of perch characteristics showed significant species differences in most cases, but ranges in values overlapped considerably. If confidence ellipses in Fig. 2 were drawn based on standard deviations instead of standard errors, overlap would be extensive. Despite this, no interspe-
cific confrontations were observed during the course of this study although a Vesper Sparrow and a Western Meadowlark perched on a particular large juniper simultaneously on several occasions. The number of perches continuously available to a bird exceeded 200 in the most restricted case and was generally >1000.

Perch-sites, by nature of their high degree of selection by birds, are important components of avian habitat, but are they or could they be potentially limiting? In the present study, 74.0% of perches used by Western Meadowlarks were chosen from a group of the highest shrubs that included only 3.5% of all available shrubs. This pattern is similar but not as dramatic for the other bird species and emphasizes preferences for high perches. It also suggests that shrubs for perching may be a potential limiting resource. Absolute numbers of perches needed by individuals have not been determined for any passerine species to my knowledge, although Lack (1933) and Lack and Vanables (1939) stated that a single tree or shrub used solely as a song perch was necessary in territories of several heathland and woodland birds.

There are several reasons why shrub perches, in most cases, would not be limiting to shrubland and grassland birds. Not all species of birds require a fixed perch for singing (i.e., Horned Lark, Western Meadowlark) and the lack of elevated perches in areas inhabited by true grassland birds may have been a selecting force in the evolution of aerial song displays. Some species (e.g., Western Meadowlark) appear to select the highest available perches in different areas and do not exhibit fixed, narrow ranges in perch heights used. Birds inhabiting grasslands lacking shrubs and requiring fixed perches (e.g., Vesper Sparrow) use grass and forb stalks from which to sing (Wiens 1969) but the same species used shrubs almost exclusively in this study when shrubs were available. In other birds (e.g., Brewer’s Sparrow), it is virtually impossible to determine if song perches are limiting because use is confounded with other functions such as nest support and feeding sites. Habitat suitability of an area for shrubland and grassland birds is certainly improved by elevated song perches but the presence of certain species may not be dependent upon them. Abundant song perches should allow males to effectively delineate, patrol, and defend boundaries of their territories.

Acknowledgments.—I thank W. K. Parker for field assistance during this study. M. W. Carter and R. Morrell provided expert advice on statistical and computer methodology. J. C. Barlow, C. L. Cink, J. T. Flinders, H. H. Frost, C. D. Jorgensen, T. Rich, H. D. Smith, and C. M. White provided helpful editorial suggestions and J. Eckensberger typed the manuscript. Funding was provided by the Department of Zoology, Graduate School, and ASBYU organization of Brigham Young University. The U.S. Forest Service provided lodging and access to records.—JOHN S. CASTRALE, Dept. Zoology, Brigham Young Univ., Provo, Utah 84602. (Present address: Indiana Division of Fish & Wildlife, R.R. 2, Box 477, Mitchell, Indiana 47446.) Accepted 10 Apr. 1983.


Observations of male woodcock on singing grounds.—American Woodcock (Scolopax minor) males have been previously reported to use two or more singing sites within a display period (Sheldon, The Book of American Woodcock, Univ. Mass. Press, Amherst, Massachusetts, 1967; Davis, Wilson Bull. 82:327–328, 1970). These observations were speculative, however, since the woodcock involved were unmarked and only appeared to be the same birds. During our study, conducted at the McClintic Wildlife Station, 11 km north of Point Pleasant, Mason Co., West Virginia, birds were color banded and positive identifications made. Woodcock using multiple sites were observed at eight locations between 4 March and 2 April 1979. Individual birds frequently were seen displaying at two or more singing
sites located 100–210 m apart. Some birds alternated between sites during the same display period, or from one day to the next. Some males appeared at auxiliary positions only when other males attempted to use these sites. A description of a typical example, which occurred on 19 March, follows: We arrived at the singing site before the display period began. A bird began “peenting” (Sheldon 1967) on site A at 05:40. Shortly thereafter a bird “peented” on site B (188 m northwest and separated from singing ground A by a row of trees and shrubs). The bird on site A flew over to site B, “cackled,” began a display flight over site A but landed on site B. He was identified on both sites as “double-green”—the bird which had displayed on site A for 13 consecutive days. The bird made another display flight and landed on site A. During the next 28 min five more flights were made, site A being used three times and B used twice. This bird alternated between these sites for several days. He frequently “cackled” on his approach to site B. Several weeks later site B became occupied and remained so for 10 days, with the double-green bird remaining on site A for an additional 24 days.

Pugnacious behavior on singing sites during the display period is not uncommon in woodcocks (Sheldon 1967; Godfrey, Ph.D. diss., Univ. Minnesota, Minneapolis, Minnesota, 1974). During this study such behavior was usually preceded by audible “peents” or “cackles” by intruding birds. On three occasions, non-displaying birds were estimated to be 0.3 m to 1 m from a displaying male. These non-displaying birds appeared to be ignored by the displaying male. All birds involved were color-banded and of known sex. One non-displaying male previously displayed on another singing site. No vocalizations were heard from the non-displaying males. If pre-copulatory calls, as described by Sheldon (1967), are necessary for female receptiveness to mating, these silent males may represent a minimal competitive challenge to dominant males trying to attract hens.—BYRON P. SHISSLER AND DAVID E. SAMUEL, Div. Forestry, West Virginia Univ., Morgantown, West Virginia 26506. Accepted 4 Mar. 1983.


Notes on the ecology of the Black-breasted Puffleg on Volcán Pichincha, Ecuador.—The 10 endemic Andean “puffleg” hummingbirds of the genus Eriocnemis include a number of little known species presently known from only one or a few adjacent mountains or from a single river valley. We here report the first detailed observations on the ecology of the endemic Ecuadorian species, the Black-breasted Puffleg (Eriocnemis nigrivestis), which is known only from Volcán Pichincha and Volcán Atacazo, two adjacent volcanic peaks less than 20 km west of Quito in north-central Ecuador.

During a 3-week search in September 1980, we located three E. nigrivestis on Cerro Pugsi, on the west slope of Pichincha. Here we conducted a brief study from 19–27 September on the habitat and feeding ecology of this little known hummingbird.

The study site was a saddle of flat ground on a ridge crest located at 3020 m elev. (for a picture of this site see Chapman, Bull. Am. Mus. Nat. Hist. 55:94, plate XIX, 1926). We observed one male daily in specific feeding areas and also sometimes heard another male individual calling: a monotonous repeated metallic “tzeet tzeet tzeet tzeet tzeet. We also found one site regularly visited by a female.

The natural vegetation on the saddle was shorter in height than the vegetation on surrounding slopes or in the valleys of the Río Mindo and Río Verdecocha, which run south and north, respectively, of Cerro Pugsi. Most canopy trees did not exceed 8–10 m in height. Dense growths of ericads and abundant epiphytes characterized the non-arborescent vegetation, but several areas on the saddle were grazed by cattle, resulting in local grassy open-
Table 1

Characteristics of Flowers of Food Plants of *Eriocnemis nigrivestis*

<table>
<thead>
<tr>
<th>Family species</th>
<th>Length of tube (mm)</th>
<th>Corolla color</th>
<th>Orientation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macleania macrantha</em></td>
<td>44</td>
<td>orange</td>
<td>pendant</td>
</tr>
<tr>
<td><em>Thibaudia floribunda</em></td>
<td>17</td>
<td>red and white</td>
<td>various</td>
</tr>
<tr>
<td><em>Disterigma cf. acuminatum</em></td>
<td>9</td>
<td>white</td>
<td>pendant</td>
</tr>
<tr>
<td><em>Disterigma acuminatum</em></td>
<td>5</td>
<td>pink</td>
<td>pendant</td>
</tr>
<tr>
<td><em>Palicourea huigrensis</em></td>
<td>20</td>
<td>blue</td>
<td>various</td>
</tr>
<tr>
<td><em>Psychotria uliginosa</em></td>
<td>8</td>
<td>white</td>
<td>various</td>
</tr>
<tr>
<td><em>Heppiella ampla</em></td>
<td>16</td>
<td>red</td>
<td>horizontal</td>
</tr>
<tr>
<td><em>Manettia recurva</em></td>
<td>5</td>
<td>white</td>
<td>various</td>
</tr>
<tr>
<td><em>Miconia corymbiformis</em></td>
<td>cup</td>
<td>pale yellow (calyx red)</td>
<td>upright</td>
</tr>
<tr>
<td><em>Miconia hymenanthera</em></td>
<td>cup</td>
<td>yellow (calyx red)</td>
<td>various</td>
</tr>
<tr>
<td><em>Burmeistera sp.</em></td>
<td>20</td>
<td>green</td>
<td>horizontal</td>
</tr>
<tr>
<td><em>Fuchsia cf. silvatica</em></td>
<td>23</td>
<td>red</td>
<td>pendant</td>
</tr>
<tr>
<td><em>Tropaeolum pubescens</em></td>
<td>24</td>
<td>pink</td>
<td>horizontal</td>
</tr>
<tr>
<td><em>Rubus sp.</em></td>
<td>cup</td>
<td>pink</td>
<td>various</td>
</tr>
</tbody>
</table>

*E. nigrivestis* bill (exposed culmen): male, $x = 15.27 \pm 0.46$, $N = 5$; female, $x = 15.82 \pm 0.47$, $N = 5$.

Voucher specimens of all plant material referred to in this paper are deposited at the Gray Herbarium, Harvard University, and the New York Botanical Gardens.

Mode of minimum distance from opening to base of corolla tube ($N = 6$).

As actually presented to hummingbird; influenced by growth form.

Horizontal to upright in panicle.

In the forest and lush second growth comprised primarily of blackberry brambles (*Rubus* sp.) where grazing was not as intensive. The most conspicuous plant in bloom in the understory was the small tree *Palicourea huigrensis* (Rubiaceae), with bright blue flowers borne on large panicles. Among the ericads were several species of *Disterigma* that formed large tangles up to canopy height as well as less conspicuous species of scrambling growth form including *Thibaudia floribunda* and *Macleania macrantha*. The undergrowth was rich with flowering herbaceous plants, creepers, and vines. During our September visit several of the more common plants appeared to be nearing the end of their flowering period; *P. huigrensis* and the ericads were heavily laden with fruit and the number of flowers decreased noticeably during our visit.
### Table 2
**Hummingbird Feeding Records**

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Male</th>
<th>Female</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrubs and scramblers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macleania macrantha</td>
<td>4</td>
<td></td>
<td>female Coeligena lutetiae (1); female Coeligena torquata (1)</td>
</tr>
<tr>
<td>Thibaudia floribunda</td>
<td>22</td>
<td></td>
<td>Diglossa lafresnayi (2)</td>
</tr>
<tr>
<td>Disterigma cf. acuminatum</td>
<td>12</td>
<td></td>
<td>Diglossa lafresnayi (2)</td>
</tr>
<tr>
<td>Disterigma acuminatum</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miconia hymenanthera</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fuchsia cf. silvatica</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rubus sp.</td>
<td>12</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Vines/climbers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heppiella ampla</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manettia recurva</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burmeistera sp.</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropaeolum pubescens</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small trees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palicourea huigrensis</td>
<td>92</td>
<td>24</td>
<td>male Coeligena lutetiae (1); Eriocnemis luciani (4); Metallura tyrianthina (5); male Heliangelus strophianus (1)</td>
</tr>
<tr>
<td>Miconia corymbiformis</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herbaceous</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Psychotria uliginosa</td>
<td>7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Most often through holes in the base of the corolla.

The few individuals of *E. nigrivestis* were the most frequently seen of the 10 hummingbird species we recorded from our study site. Other regular species on the saddle were Mountain Velvetbreast (*Lafresnaya lafresnayi*), Buff-winged Starfrontlet (*Coeligena lutetiae*) and Tyrian Metaltail (*Metallura tyrianthina*), while species seen rarely included the Sword-billed Hummingbird (*Ensifera ensifera*), Collared Inca (*Coeligena torquata*), Sapphire-vented Puffleg (*Eriocnemis luciani*), Gorgeted Sunangel (*Heliangelus strophianus*), Purple-backed Thornbill (*Ramphocichla microhynchus*), and Speckled Hummingbird (*Adelomyia melanogenys*).

We recorded food plants for *E. nigrivestis* during walks over the study area and by extended watches at preferred feeding sites. Feeding records were tabulated according to the methods in Snow and Snow (Bull. Br. Mus. Nat. Hist. [Zool.] 38:105–139, 1980). Floral characteristics of food plants are given in Table 1 and feeding records are given in Table 2. Males fed in a wide variety of microhabitats but mostly in low dense vegetation (less than 2 m). Low foraging may cause some underrepresentation of certain understory nectar sources but *P. huigrensis* was by far the most frequently visited nectar source for both sexes. We
Fig. 1. Quito area showing localities mentioned in the text. Pichincha is comprised of a series of peaks of which the two major ones, Guagua Pichincha and Rucu Pichincha, are shown.

recorded the female feeding only in a grove of *P. huigrensis* which had few alternative nectar sources so male-female differences in diet breadth may be an artifact. Most of the major food plants (more than 10 records) had straight tubular corollas of the general size and shape of the *E. nigrivestis* bill (see Table 1). Feeding was usually through the corolla opening, including *P. huigrensis*. However, males fed through holes made by them or presumably the
Glossy Flower-piercer (*Diglossa lafresnayii*) at the corolla base of *M. macrantha*, which had tubular flowers much longer (44 mm) than their bills (\( \bar{x} = 15.3 \text{ mm}, N = 5 \)). Both sexes frequently perched on adjacent branches or leaves (often at *P. huigrensis*) while flower feeding or sat in the leaf litter when feeding at prostrate vines of *Heppiella ampla*.

We conducted extended watches of a male *E. nigrivestis* in a plot of natural vegetation roughly 20 \( \times \) 20 m, in which the male fed at 11 plant species. The male was regularly but intermittently present within this plot throughout watch periods, which lasted from 07:00–16:30 on two separate days. During this time the male would regularly station himself at the top of a small (4 m) tree located in the northern portion of the plot near a large stand of *P. huigrensis*. Visits to this or nearby secondary perches were usually accompanied by extended feeding bouts, invariably at the *P. huigrensis* stand. Continuous time on the principal perch ranged from a few seconds to over 9 min, but was usually between 2 and 4 min duration. The male never vocalized from any of these perches but did catch insects and chased other hummingbird species, including females of *C. lutetiae*, *E. ensifera*, *M. tyrianthina*, and the Glossy Flower-piercer. An extended watch of the female feeding in the grove of *P. huigrensis* between 07:00 and 15:00 showed regular visitation throughout the day but less total time in her feeding area than the male for the same period (male: 131 min perching, 60 feeding bouts; female: 17 min perching, 18 feeding bouts). The female adopted inconspicuous perches and never chased other hummingbirds in the area.

During our 3-week survey of Pichincha, we spent time at a variety of different elevations from 2650–4200 m, a good cross-section of the upper vegetated habitats on Pichincha. We recorded *E. nigrivestis* only on the crest of Cerro Pugsí; the few individuals were strictly limited to this ridge crest, despite flowering *P. huigrensis* elsewhere between 2850–3200 m. The northern and western slopes of Pichincha below the various peaks show a characteristic topography of high narrow ridges or "nudos" running roughly east-west, between which are deeply incised river valleys (a brief trip to Atacazo, the only other locality where *E. nigrivestis* has been recorded, substantiated the presence of similar topography there as well). Within this ridge-valley system, the distribution of *E. nigrivestis* appears to parallel the ridge crests. In addition to our findings for the few individuals on Pugsí, M. Olalla has found *E. nigrivestis* in the past only on the tops of the nudo ridges: specifically on Cerro Pugsí and Frutillas on the northwest slope of Pichincha, and the Cordillera Alaspungo to the north, across the Rio Alambi (see Fig. 1). The ridge crest vegetation at these elevations, as described here, is characteristically denser and shorter and with greater representation of ericas than the vegetation on the surrounding slopes and seems to comprise a structurally and floristically distinct habitat required by *E. nigrivestis*.

The total elevational distribution of *E. nigrivestis* on Pichincha appears to be broad, but the limited information available suggests that it may be complicated by sexual differences and seasonal movements. Males have been reported between 3650 and 4725 m by Goodfellow (Oberholser, Proc. U.S. Natl. Mus. 24:309–324, 1902) during November to January (USNM specimens examined by R.B.) and at other months at lower elevations: around Verdecococha (approx. 2850 m; Paynter and Traylor, Ornithological Gazetteer of Ecuador, Harvard College, Cambridge, Massachusetts, 1977) in July (ANSP specimens examined by R. B.), "above Gualca" at 2750 m and Cerro Pugsí in June (AMNH specimens examined by R. B.) and Cerro Pugsí at 3020 m in September (this study). In contrast, females have been collected from as low as 2400 m in June, "above Gualca" (AMNH specimens examined by R. B.) and up to 3300 m at Yanacocha (P. Greenfield, pers. comm.) (see Fig. 1) but have not yet been recorded higher. Further fieldwork will be needed to verify both the presence of males alone at the highest elevations, which are based solely on the old Goodfellow records, and the elevational migration suggested by the complementary collecting dates for low and high elevations, at least for males if not in both sexes. It is possible that elevational migration by
E. nigrivestis is timed to coincide with flowering of P. huigrensis (and other plants) which bloom seasonally at lower elevations.

The general ecology of E. nigrivestis is similar to that recorded for the closely related species, the Glowing Puffleg (E. vestitus) (Snow and Snow 1980). Snow and Snow (1980) observed E. vestitus feeding principally at plants of similar general morphology (straight tubular corollas 10–20 mm in length) in similar taxonomic groups (Cavendishia: Ericaceae more often than Palicourea: Rubiaceae for E. vestitus). Territoriality in E. vestitus was pronounced while this was only suggested in the male E. nigrivestis we observed, perhaps a seasonal effect. Finally E. vestitus, like E. nigrivestis, did not occur in tall forested habitats at similar elevations (Snow and Snow [1980] study at 2400–2500 m).

The evidence presented here suggests that the greatly restricted range of E. nigrivestis is not due to dietary specializations. Male nectar sources are from a broad spectrum of plants, and the principal food plant of both sexes, P. huigrensis, is a widespread Andean species. Nesting requirements of E. nigrivestis may still be threatened with extinction through habitat destruction, especially if the species requires specific habitats of natural vegetation at certain times of year, such as that found at nudo ridge crests. The vegetation on nudos in particular is rapidly disappearing because nudos provide flat ground for cultivation in otherwise precipitous terrain. In light of its restricted range and the threat of habitat destruction resulting from such close proximity to a major urban center, Quito, we consider E. nigrivestis an endangered species.

Acknowledgments.—R. Bleiweiss would like to acknowledge the generous support of World Wildlife Fund U.S. for his fieldwork in Ecuador and the assistance of the Departamento de Parques Nacionales y Vida Silvestre of Ecuador, especially Dr. Sergio Figueroa. Laszlo Meszoly kindly drew the map. Examination of museum specimens was possible through the generous cooperation of J. Bull (AMNH), F. B. Gill (ANSP), R. A. Paynter, Jr. (MCZ), and R. L. Zusi (USNM). J. Luteyn (New York Botanical Gardens), L. Skog, and J. Wurdack (National Museum of Natural History) kindly identified the plant material. Frank B. Gill, J. V. Remsen, Calvin Sperling, and François Vuilleumier provided helpful comments on an earlier draft of this paper.—ROBERT BLEIWEISS, Museum of Comparative Zoology, Harvard Univ., Cambridge, Massachusetts 02138, AND MANUEL OLALLA P., Dpto. de Parques Nacionales y Vida Silvestre, Dirección General de Desarrollo Forestal, Ministerio de Agricultura y Ganadería, Quito, Ecuador, S.A. Accepted 22 Mar. 1983.


A giant hummingbird from Paramo de Chingaza, Colombia.—On 10 October 1981, during an ornithological survey at 3250 m elev. near Laguna de Chingaza, Dept. Cundinamarca, Colombia, the senior author watched a large, perched hummingbird for 30 sec at 3 m distance; while observing it, the bird was drawn and described. The bird finally took off, ascended steeply 10–15 m and descended with spread tail in an apparent territorial display flight, to disappear in dense forest. Familiar with the Giant Hummingbird (Patagona gigas) from field studies in Peru, the observer immediately recognized the bird as a probable Patagona sp. by its size and its erratic and slow wingstrokes. However, the colors were different from those of P. gigas gigas and P. g. peruviana of which large series have been examined by Fjeldsa. The top of the head was fuscous except for white spots near the eyes; the mantle and scapulars were blackish (fuscous black?) with a green lustre rather than the normal olive or bronzv of a Giant Hummingbird; the wings were fuscous black without noticeable light feather edges and without the blue gloss of a Great Sapphirewing (Pterophanes cyanopterus). These parts were in contrast with the uniform cinnamon or cinnamon-
rufous hue of the lower cheeks, chin, throat, breast, and flanks. This color appeared only slightly brighter than that of adult P. g. peruviana, but was very different from the cinnamon-drab of P. g. gigas, and the numerous green disks of the sapphirewing female were lacking. The undertail coverts were light, the tail long, deeply forked, and darkest distally. Details of these parts mentioned were not noted precisely, but were probably as in a Giant Hummingbird. The bill was straight and probably thinner than in known Giant Hummingbirds.

The junior author sighted a bird which corresponded to the above description during botanical studies 9–13 March 1981 at Chuza, 3050 m elev., fully 10 km north of Laguna de Chingaza (Rodrigues and Barbosa, duplicated report, INDERENA, Bogota, Colombia, 1981). The bird was watched at a distance of 3 m as it fed hovering from tarflowers (Befaria glauca).

The two observations thus suggest that Paramo de Chingaza is inhabited by a probable Patagona sp. of distinctive appearance. For lack of collected specimens, we refrain from formally naming it.

Sight of a probable Patagona in Chingaza is noteworthy first of all because the place lies 900 km outside the known range of the Giant Hummingbird and secondly because the northernmost parts of the known range in Ecuador may have been colonized rather recently from the south (Ortiz-Crespo, Ibis 116:347–359, 1974), and thirdly because the habitat is unusual for a Giant Hummingbird. Patagona g. peruviana occur on open hillsides grown with agaves (Agave americana), bromeliads of the genus Puya, and varius caetic, from which they take nectar (Ortiz-Crespo 1974). Paramo de chingaza is intersected by deep valleys characterized by a tropical zone climate that produces extreme cloud cover and mists in the mountains. The annual precipitation there is 2000–3500 mm. The mountain slopes to well above 3000 m elev. are covered by low, but very dense, cloud-forest entangled by epiphytic mosses, lichens, bromeliads, orchis, and ferns. Agaves are lacking in the woodland, but a large species of Puya grows in boggy glades in bamboo vegetation (Chusquea), and two additional species occur higher up in the paramo vegetation.

On the first mentioned observation site, forest grew only on steep slopes, other areas having been cleared and in part grazed by cattle. The hummingbird seen here was perched in a tree near a forest edge. The wood abounded in flowering mistletoes (Aetaanthus mutisii), and there were many flowering Ericaceae bushes and shrubby St.-John’s-worts (Hypericum sp.) along its edge. Puya cryptantha occurred a few hundred meters uphill. Other nectivorous species included Sparkling Violetear (Colibri coruscans), Tourmaline Sunangel (Heliangelus exotis), Black-tailed Trainbearer (Lesbia victoriae), Glowing Puffleg (Erioenemis vestitus), flowerpiercers (Diglossa cf. lafresnayi), and large sphingid moths. The observation site at Chuza was in a densely wooded area, at the edge of a 2-m tall shrub near forest edge dominated by palo bolo (Brunellia sp.), Weinmannia sp. (Commiaceae), balsam-apples (elusia sp.), holly (Ilex sp.), and laurel (Vetricandra sp.).

Three new specimen records of birds for El Salvador.—During a field survey in the mountains of El Salvador on behalf of the Museum of Natural History of El Salvador, specimens were secured of three species of birds not previously taken in the country (Rand and Traylor, Manual de las aves de El Salvador. Univ. de El Salvador, 1954). Relatively little ornithological work has been done in the mountains of El Salvador because most of them have been cleared for cultivation; it is interesting that these species still manage to survive in these mountains or perhaps occasionally wander there from Guatemala or Honduras. The specimens reported here are deposited in the Royal Ontario Museum (ROM) and in the author’s private collection (VH).
Maroon-chested Ground-Dove (*Claravis mondetoura*).—An adult male (field no. RZ-11) was taken in June 1979 by R. Zaldivar on Cerro Cacahuatique, Departamento de Morazan (13°45'N, 88°12'W; elev. 1600 m) along a grassy trail in a coffee plantation. Feather replacement was noted among the left outer rectrices, but no body molt was detected. The left testis measured 4 × 2 mm. At present this specimen is in my private collection tentatively assigned to the subspecies *C. mondetoura salvini*. This race was described from Guatemala, and Honduran birds have also been assigned to it (Van Rossem, Trans. San Diego Soc. Nat. Hist. 8:5–8, 1934; Monroe, Ornithol. Monogr. 7:135, 1968).

Belted Flycatcher (*Xenotriccus calizonus*).—A sub-adult male (field no. VH-32) was mist netted by VH on 14 February 1980 at El Encinal, Distrito Forestal y de Fauna, Metapan, Departamento de Santa Ana (14°24'N, 89°24'W; elev. 1550 m) along a trail in a dense second growth oak-pine forest. Two other birds were mist netted 9 July 1980 at the same locality as the first specimen. One very young bird escaped and the other, an immature male, ROM no. 138701, was preserved as a study skin. A third specimen was
obtained 10 July 1980 and deposited in the Museum of Natural History El Salvador, but unfortunately data from this specimen were not available to me. This species is not only new for El Salvador, but has not been previously reported south of Guatemala. A female of this species taken 5 miles northwest of Purulha, Baja Vera Paz, Guatemala (elev. 1200 m) appears to be the southernmost previously known record (Land and Wolf, Auk 78:94–95, 1961).

Red-faced Warbler (Cardellina rubrifrons).—An adult male (field no. VH-31) was obtained at El Encinal 14 February 1980 by me and is also in my private collection. W.A. Thurber mentions (pers. comm.) three earlier observations of this easily identified warbler, at Cerro Verde, Departamento de Santa Ana (13°49'N, 89°38'W); one by Thurber on 10 November 1971; another by B. L. Monroe, Jr., on 4 January 1972; and the third by a visitor, R. Greenberg on November 1976. Land (Birds of Guatemala, Livingston Publ. Co., Wynnewood, Pennsylvania, 1970:301) found this species wintering in the highlands of Guatemala, and Monroe (1968:341) found it in the western highlands of Honduras.

Acknowledgments.—I wish to thank every person who helped me with the manuscript, especially Dr. Walter A. Thurber, the late Dr. Eugene Eisenmann for his aid in identifying the ground-dove, and Dr. Francisco Serrano, Director of Parques Nacionales de El Salvador, for providing transportation and personnel during the field work. I thank the Martinez family at Los Planes de Montecristo for their hospitality and my wife Nicole for her encouragement.—VICTOR HELLEBUYCK, Dept. Biology, Bishop's University, Lennoxville, Quebec J1M 1Z7, Canada. Accepted 10 Jan. 1983.


Territories of Rufous-sided Towhees contain more than minimal food resources.—Birds may be defending territories that supply more than minimal resources for survival. Empirical support for this in species defending large multi-purpose territories comes from three observations. (1) During the nestling stage when food requirements are greatest, territory size is small compared to other stages of the breeding cycle (e.g., Yarrow, Auk 87: 359–361, 1970; Wasserman, Wilson Bull. 92:74–87, 1980). Perhaps food is not limiting, since at the time eggs hatch food is abundant and the territory size need not be large (e.g., Perrins, Ibis 112:242–255, 1970). (2) On some islands the sizes of territories are much smaller than the sizes of conspecific mainland territories (e.g., Morse, Condor 79:399–412, 1977). Beer et al. (Wilson Bull. 68:200–209, 1956) suggested that the mainland birds normally would be able to subsist in a small territory, but because of the aggressive pressures of conspecifics (unrelated to food supply) their territories are much larger than the island territories. Possibly territories are smaller on islands because of the absence of species with similar diets. (3) The breeding populations of Great Tits (Parus major) during one breeding season were considerably higher than they were during any other year (Lack, Population Studies of Birds, Clarendon Press, Oxford, England, 1966). Lack argued that populations could not have been limited by resources in other years. Tompa (Auk 79:687–697, 1962) reported a similar circumstance in Song Sparrows (Melospiza melodia); in one year breeding density of sparrows was greater than average with no apparent change in food availability. Knapton and Krelis (Can. J. Zool. 52:1413–1420, 1974) presented evidence indicating that size of territories is proximately determined by the number of individuals attempting to settle and not by food availability.

Researchers suggesting birds defend territories that supply just enough resources for survival usually point out that: (1) territory size is inversely related to food availability (e.g., Stenger, Auk 75:335–346, 1958); and/or (2) breeding density is directly related to food availability (e.g., Zach and Falls, Can. J. Zool. 53:1669–1672, 1975). A few field experiments have
involved an attempt to manipulate food availability. Miller et al. (pp. 323-335 in Animal Populations in Relation to Their Food Resources, Blackwell, Oxford, England, 1970) with the Red Grouse (*Lagopus lagopus*) and Krebs (Ecology 52:2-22, 1971) with Great and Blue (*P. caeruleus*) tits found that after food was added there was either a decrease or no change in population density (territory size was not measured directly).

When Franzblau and Collins (Oecologia 46:164-170, 1980) added food to the territories of Rufous-sided Towhees (*Pipilo erythrophthalmus*) (increasing invertebrate biomass by approximately 96%) they found no change in territory size and no difference between the sizes of five experimental territories and five control territories. They concluded that size of territory was not a function of the immediate food supply.

In the present study I eliminated certain amounts of food in the territories of breeding pairs of Rufous-sided Towhees. The lack of a significant increase in territory size or decrease in breeding success after treatment suggests that these territories contained more than minimal food resources.
TABLE 1
TERRITORY SIZES BEFORE AND AFTER 10% OF THE TERRITORY WAS EXPERIMENTALLY REDUCED

<table>
<thead>
<tr>
<th></th>
<th>Before</th>
<th>After</th>
<th>Mann-Whitney U-test* U-values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x ± SE (N)</td>
<td>x ± SE (N)</td>
<td></td>
</tr>
<tr>
<td>Nestling stage</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pair 1 male</td>
<td>4120 ± 840 (3)</td>
<td>4460 ± 1130 (3)</td>
<td>6</td>
</tr>
<tr>
<td>female</td>
<td>3130 ± 500 (3)</td>
<td>3270 ± 650 (3)</td>
<td>5</td>
</tr>
<tr>
<td>Pair 2 male</td>
<td>2970 ± 640 (4)</td>
<td>2660 ± 610 (3)</td>
<td>7</td>
</tr>
<tr>
<td>female</td>
<td>1260 — 1 (1)</td>
<td>1270 ± 90 (2)</td>
<td>2</td>
</tr>
<tr>
<td>Pair 3 male</td>
<td>2810 ± 330 (7)</td>
<td>2990 ± 300 (4)</td>
<td>17</td>
</tr>
<tr>
<td>female</td>
<td>4880 ± 1350 (3)</td>
<td>5660 ± 930 (3)</td>
<td>7</td>
</tr>
<tr>
<td>Fledgling stage</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pair 1 male</td>
<td>6970 ± 1190 (6)</td>
<td>6540 ± 1280 (3)</td>
<td>9</td>
</tr>
<tr>
<td>female</td>
<td>2400 ± 700 (4)</td>
<td>3770 ± 930 (6)</td>
<td>15</td>
</tr>
</tbody>
</table>

* All comparisons P > 0.30.

Methods.—During the spring and summer of 1979, 1980, and 1981, I observed 16 breeding pairs of Rufous-sided Towhees at the Massachusetts Broadmoor/Little Pond Wildlife Sanctuary in South Middlesex Co., Massachusetts. I divided each territory into 10 by 10 m quadrats and recorded a bird’s predominant activity and location, placing its position on a grid. I estimated territory size by using the computer program of Koeppel et al. (J. Mammal. 56:81–90, 1975). The program gives an ellipse for a series of observations. One observation each minute for 100 min of foraging represented estimates of territory size before and after manipulation.

The breeding pairs of towhees were selected so that each had a territory that was not completely constrained by adjacent territories. On at least one border there was room for expansion into unused habitat.

Ten, 20, 30, or 50% of available feeding area in each territory was made inaccessible to the birds by randomly placing 10-m² clear polyethylene sheets and/or crop-protection netting in quadrats (making invertebrate prey unavailable to the birds). The birds seemed to forage uniformly within each 100-m² quadrant. For the manipulations one, two, three, or five 10-m² sections were eliminated from each quadrant by choosing section positions from a random numbers table (each quadrant was composed of ten 10-m² sections). The placing of the sheets and treatments were applied on days 4–6 of the nestling stage of 15 pairs of birds and during the fledgling stage of one pair. Days 1–3 in each stage served as controls for the respective manipulations. I used a Kruskal-Wallis test to determine if there was a difference in percent change in territory size during the nestling stage among the 0, 10, 20, 30, and 50% groups.

For the situation where 10% of the territories was made unavailable to territory holders I used a Mann-Whitney U-test to compare the territory sizes of individual birds (male and female of three pairs, Table 1) before and after manipulation (the numbers of 100-min replicates for the other territory reduction groups were too small to test in this fashion). To test for a difference between male and female territory size before manipulation (days 1–3 in each nestling stage, 15 pairs of birds) I used a Wilcoxon paired-sample test.

Results.—There was a significant difference in percent change in territory size during the nestling stage among the 0, 10, 20, 30, and 50% groups (Fig. 1; Kruskal-Wallis test, P <
0.01). Birds whose available foraging area was reduced by 50% increased the size of their territories to a greater degree than the other four groups (P < 0.05, nonparametric multiple comparison: Zar, Biostatistical Analysis, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974). There was no significant difference in percent increase in territory size among the 0, 10, 20, and 30% groups.

After 10% of the available foraging area was made inaccessible to the birds in the nestling stage there was no significant change in territory size for either the male or female in the three pairs studied (Table 1). On average males increased their territories 1.4% (N = 3) and the females 7.1% (N = 3). Before manipulation average male territories (t = 5220 ± 1450 m², N = 15) were not statistically significantly larger than female territories (t = 4460 ± 1660 m², N = 15). In the pair studied during the fledgling stage there was a 6.1% decrease in the size of the male’s territory and 57.1% increase in the size of the female’s territory (Table 1).

Discussion.—Hinde (Behaviour Suppl. 2, 1952) found that when winters in England are unusually mild, Great Tits remain territorial; but if conditions become more severe, they form social groups. On warm days in late winter they will, at least temporarily, settle within their territories, possibly responding to the lowered energy requirements of mild days. Carpenter and MacMillen (Science 194:639-642, 1976) found that Hawaiian Honeycreepers (Vestiaria coccinea) shifted from territorial to non-territorial states in response to size of nectar supply and competitive pressure. Alterations of Rufous-sided Towhee territories were made when energy demands should be highest and response to limitation of food source should occur. Fluctuations in territory size from one stage in the breeding cycle to another are common in many species (e.g., Stefanski, Condor 69:259-267, 1967).

There have been few experimental, manipulative avian studies which attempt to determine if birds defend territories that supply more than minimal food resources. Featherstone (M.Sc. thesis, Univ. Toronto, Toronto, Ontario, 1966), using pesticides, decreased the foraging area of individual Ovenbirds (Seiurus aurocapillus) by 42% and found that the birds increased the size of their territories 38%. He concluded that the size of Ovenbird territories is at least partially determined by the amount of food present.

My results indicate that when 0, 10, 20, or 30% of the territories was made unavailable an adequate food supply was still available. Only when 50% of the territory was made unavailable was there a substantial increase in the territory size. There are at least two explanations for this result. One is that the function of territoriality is more than the procurement of a food resource. Territorial behavior in the Rufous-sided Towhee may also be a means of preventing sexual interference from conspecifics. An alternative, but not a mutually exclusive one, is that the birds are defending territories that contain more food than they can consume as insurance against a bad year.

Acknowledgments.—This research was supported by a Public Health Service Grant (MH 33824-01). I would like to thank B. Lund and the Massachusetts Audubon Society for their cooperation during the course of this research. For help of various kinds I would like to thank P. V. August, R. H. Tamarin, L. Whiteside, and R. Zach.—Fred E. Wasserman, Dept. Biology, Boston Univ., Boston, Massachusetts 02215. Accepted 31 Aug. 1982.


The shoulder-spot display in male Blue Grouse.—A “shoulder-spot” display has been described for both males and females of several species of grouse (Lumsden, Living Bird 9:65-74, 1970). The shoulder spot is formed by exposing the white underwing coverts at the proximal end of the humerus on the upper surface of the wing (Lumsden 1970). Movement of the patagial skin may also be important in effecting this display (Garbutt.
TABLE 1

SEQUENTIAL ANALYSIS OF PRECEDING DISPLAY/FOLLOWING REACTION FOR INTERACTIONS BETWEEN YEARLING AND ADULT MALE BLUE GROUSE

<table>
<thead>
<tr>
<th>Preceding display</th>
<th>Following reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoulder spot</td>
<td>Signaller</td>
</tr>
<tr>
<td></td>
<td>Attack</td>
</tr>
<tr>
<td>25</td>
<td>15</td>
</tr>
</tbody>
</table>

Wilson Bull. 93:98-99, 1981). This display in males has been associated with copulatory, ambivalent (or conflict), avoidance, and aggressive behaviors (Lumsden 1970; Hjorth, Viltrevy 7:184-596, 1970; McNicholl, Ph.D. thesis, Univ. Alberta, Edmonton, Alberta, 1978; Garbutt 1981). However, descriptions of the display in the above studies have come primarily from observations of birds in unnatural situations such as disturbance by humans, interactions between birds in avaiaries, encounters with mirror images during field studies, or responses to male and female dummies. Most reports lack description of the behavioral activities of the interacting birds before and after the display and also lack details of age and breeding status of the birds involved.

In 1980 and 1981, I recorded the movements and behavior of 24 yearling male Blue Grouse (Dendragapus obscurus) fitted with radio transmitters on Hardwicke Island, British Columbia. Age of birds was categorized as yearling (10–15 months of age) and adult (>15 months of age) based on the shape, color, and condition of the outer primaries (Braun, Outdoor Facts No. 86, Colorado Dept. Nat. Resour., 1971). Observations of birds were made with the aid of binoculars, using vegetation as natural blinds. If a bird was disturbed by my presence, details of activity were not recorded until he appeared to resume normal behavior such as feeding or preening. Radio transmitters appeared to have no effect on the behavior of birds. Observations were carried out from early April to mid-June in both years, and totalled 106 h.

Yearling males are rarely territorial. Rather, they associate with a few territories occupied by adult males (Jamieson and Zwickel, Auk 100:653-657, 1983). I observed yearling males interacting with territorial adult males 25 times. In each case, when the adult male detected a yearling on or near his territory, he immediately assumed a “feather spread” display posture (Stirling and Bendell, Syesis 3:161-171, 1970), then ran or flew toward the yearling. When 1–3 m from the yearling, the adult assumed a threat posture (McNicholl 1978) in which the feathers were laid flat against the body, the tail was lowered, the eye combs were red or orange, and white shoulder spots were visible. The adult quickly moved back and forth in front of and around the yearling, and on 11 occasions gave a “growl” (Stirling and Bendell 1970), an aggressive or threat call. When approached in this manner, yearlings invariably assumed a neutral posture (McNicholl 1978) and were never seen to display the shoulder spot during these encounters. On 10 occasions, the yearling remained in a neutral posture for 10–30 sec before flying from the area. In 14 other instances, the adult eventually rushed at the yearling and displaced him. I saw only one physical attack in which an adult pecked at the back of a yearling, removing several feathers.

On two occasions, two yearling males were seen to interact. In each case, both birds assumed threat postures with shoulder spots displayed before one displaced the other. I observed 11 instances of yearling males and 10 of territorial adult males courting females. I never saw shoulder spots in any of these cases.
Lumsden (1970) reported that male Blue Grouse display shoulder spots before and while attacking their images in a mirror. He concluded that the display may express fear in conflict with other behavioral states. McNicholl (1978) saw Blue Grouse displaying shoulder spots in various alert postures, at the approach of an observer while the male was courting a female, and during aggressive interactions. He suggested that the display represents fear, and perhaps subordination, in conflict situations. Hjorth (1970) observed shoulder spots on territorial Blue Grouse that were moving in the vicinity of an intruder. However, in summarizing the function of this display for grouse in general, he suggested that it is associated with subordination and avoidance behaviors.

It is sometimes difficult to interpret the signal content of a behavioral display. By using sequential analysis it may be possible to infer tendencies associated with given postures (Slater, pp. 131–153 in Perspectives in Ethology, Vol. 1, P. P. G. Bateson and P. H. Klopfer, eds., Plenum Press, New York, New York, 1973). For example, if the shoulder-spot display signalled fear or subordination, as some researchers have suggested, one would expect the signalling bird to retreat or act submissively after showing the display. Likewise, the receiver would not be expected to retreat or be attacked. Yet, Table 1 rather strongly implies that the shoulder-spot display signals aggression. This display was often followed by an attack by the signalling bird and invariably by the retreat of the receiver. Furthermore, the display was primarily given by territorial adult males when confronting non-territorial yearling males that had intruded on or near their territory. These observations suggest that under natural conditions the shoulder-spot display of male Blue Grouse is associated with aggressive behaviors and may function as a threat display. However, for other species of grouse this display may serve different functions. More observations of birds in natural situations are needed before further speculation on the evolutionary development of the shoulder-spot display and its role in the behaviors of various grouse species.

Acknowledgments.—F. C. Zwicker, J. F. Bendell, and A. Middleton provided useful comments and criticism. I thank J. L. Craig for suggesting the use of sequential analysis. Financial support for the study came from the Natural Sciences and Engineering Research Council of Canada, the National Sportsman’s Fund, the British Columbia Fish and Wildlife Branch, and the University of Alberta.—I. G. JAMESON, Dept. Zoology, Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada. (Present address: Dept. Zoology, Univ. Auckland, Auckland, New Zealand.) Accepted 5 May 1983.


Nestling growth relationships of Brown-headed Cowbirds and Dickcissels.—Data on nestling growth of brood parasites and their hosts are surprisingly few in the literature. Even the Brown-headed Cowbird (Molothrus ater), whose host relations have been studied in some other respects, has not been studied in any detail from this standpoint. This is particularly regrettable because the lack of host specialization and high incidence of multiple parasitism in this species recommend it for intensive studies of parasite-host growth relationships. Isolated or fragmentary records of growth in cowbirds are available in Friedman (The Cowbirds, C. C. Thomas, Springfield, Illinois, 1929), Pickwell (Trans. Acad. Sci. St. Louis 27:1–160, 1931), Herrick (Wild Birds at Home, Appleton-Century, New York, New York, 1935), Nice (Trans. Linn. Soc. N.Y. 4, 1937; Wilson Bull. 51:233–239, 1939), Mayfield (The Kirtland’s Warbler, Cranbrook Inst. Sci., Illinois, 1960), and Nolan (Ornithol. Monogr. No. 26, 1978). Hann (Wilson Bull. 49:145–237, 1937) illustrated the growth of five cowbirds raised in three nests of the Ovenbird (Seiurus aurocapillus), Norris (Wilson Bull. 59:83–103, 1947) provided data for five individuals raised by different host species, and Scott (Wilson
Bull. 91:464–466, 1979) presented pooled growth data for nine individuals raised by three different host species. King (Auk 90:19–34, 1973) measured the growth of Shiny Cowbirds (Molothrus bonariensis) in nests of Rufous-collared Sparrows (Zonotrichia capensis) and found that broods of two cowbirds grew at a substantially slower rate than broods of one. He suggested that Z. capensis could rear a maximum of two cowbirds or four sparrows, or an equivalent combination.

In 1974 I collected data on the growth relationships of Brown-headed Cowbirds and Dickcissels (Spiza americana) in prairie habitat in eastern Kansas (Konza Prairie Research Natural Area). The intensity of cowbird parasitism in this study was extremely high—I found nests containing as many as nine cowbird eggs and three host eggs. More than one cowbird was evidently laying in many of the nests, behavior that may present some intricate evolutionary problems with respect to clutch-size manipulation by cowbirds. Fifty-nine of 65 nests were parasitized (91%), and the mean number of cowbird eggs per parasitized nest was 3.1 (SD = ±1.74). Dickcissels raised up to five young in mixed broods of various composition. Brood composition at fledging in 27 successful nests (42% of the total) averaged 1.6 Dickcissels and 1.3 cowbirds.

I visited nests every other day and weighed young to the nearest 0.1 g with a Pesola spring balance. I estimated the ages of nestlings hatched between visits to the nearest day by tarsal measurements. Because the frequency of visits seemed to induce premature nest leaving in many instances, my data on weight gain are adequate for analysis through only about the first week of the nestling period. The measure of growth I use is the weight of a nestling on day 7 (cowbirds, N = 22) or day 6 (Dickcissels, N = 33; differences in initial weight at hatching were negligible within species). I regressed these values on the number of cowbirds (Nc) and the number of Dickcissels (Nd) in the broods from which the measurements were obtained. I also included date of hatching (X3) as an independent variable since there was a seasonal decline in growth rates. The analysis for cowbirds yielded the following multiple regression equation (P < 0.05):

\[ \text{Weight day 7 (g)} = 35.3 - 2.67X_1 - 1.64X_2 - 0.18X_3. \]

Each of the independent variables contributed significantly to the regression (P < 0.05), which has an R value of 0.658. Thus, the body weight of cowbirds a week after hatching was inversely related to the number of competitors in the nest, and another cowbird had a considerably larger effect than a competing host nestling. In contrast, there was no significant relationship between the weights of host nestlings and either the number of conspecifics or the number of parasites in the brood. This could arise if Dickcissels showed greater overall variability in age-specific weights, thus requiring a larger sample to detect the effects of brood-size and composition. However, coefficients of variation for the weights of cowbirds and Dickcissels were 0.144 and 0.103, respectively (P < 0.11, cf. Sokal and Braumann, Syst. Zool. 29:50–66, 1980).

These results raise the interesting possibility that Dickcissels and other species may preferentially feed their own young as an adaptive response to brood parasitism. Vocal mimicry of begging calls is common in some groups of brood parasites (Payne, Ann. Rev. Ecol. Syst. 8:1–28, 1977), and Rothstein (Auk 95:152–160, 1978) found geographical variation in the moult coloration of nestling cowbirds which he suggested is an incipient adaptation to prevent detection by various hosts. It would not be surprising to find that some of the cowbird’s hosts are adapting to brood parasitism through discrimination at feeding time.

There is, however, an alternative explanation for the insensitivity of Dickcissel growth to cowbird parasitism, with rather different implications for the parasite. S. D. Fretwell (pers. comm.) has observed that some passerine species feed the smaller members of a brood preferentially during the latter part of the nestling period and has developed a mathematical
model to show when this should occur. (Such behavior is, of course, the opposite of brood reduction by selective starvation.) To the extent that this occurs, the difference in size between cowbirds and most of their host species would be less advantageous for the parasite than is usually supposed. Notably, Elliott (Auk 95:161–167, 1978) reported that one of the cowbird's largest hosts, the Eastern Meadowlark (Sturnella magna), appeared better able to feed more than one cowbird per nest than two smaller host species. The mean number of cowbird eggs per nest was higher for meadowlarks than for the smaller hosts in the same study. With data presently available, however, I can only suggest that growth of brood parasites and their hosts may be influenced to a considerable degree by behavioral interactions.

Considering the results of the present work and theoretical interest in growth of brood parasites and their hosts, recommended further studies would include: (1) thorough study of growth in a nonspecialized brood parasite such as the Brown-headed Cowbird and a full range of its hosts with respect to body size, growth rates, and behavior; (2) experimental manipulation of brood-size and composition; and (3) direct observations of feeding activity to determine if adults feed their own young or the smaller of the brood preferentially.

Acknowledgments.—The fieldwork in Kansas was supported by an undergraduate research program at Kansas State University funded by the National Science Foundation. I wish to acknowledge the cooperation of the director, Konza Prairie Research Natural Area, and to thank J. L. Zimmerman, S. D. Fretwell, and P. F. Elliott for supervision and discussion during my tenure at KSU. R. K. Colwell, A. Heyneman, F. A. Pitelka, and D. W. Winkler commented helpfully on portions of an earlier draft of the manuscript.—Scott A. Hatch, Museum of Vertebrate Zoology and Dept. Zoology, Univ. California, Berkeley, California 94720. (Present address: U.S. Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, Alaska 99503.) Accepted 15 Mar. 1983.

Wilson Bull., 95(4), 1983, pp. 671–672

A Common Loon nest from Minnesota containing four eggs.—On 12 June 1982 we found a Common Loon (Gavia immer) nest containing four eggs. The nest was located on a lake approx. 50 ha in size, 25 km NE of Bemidji, Beltrami Co., Minnesota, and was situated about 30 m from shore on a mat of floating vegetation. Two adult loons, the only loons observed on the lake, were nearby and were diving repeatedly within 40–60 m of the nest. When we visited the nest 6 days later it was destroyed. The large end had been broken away from one egg and the contents removed except for a small amount of albumen that still appeared fresh. The other three eggs were found intact in shallow water adjacent to the nest. Two loons were observed on the opposite side of the lake. The eggs were collected and placed in a refrigerator. Later, they were measured, weighed, and examined for fertility.

The four eggs were similar in size to those measured by other authors (Table 1). Weights of the three whole eggs were 140, 144, and 146 g, respectively. Nearly equal volume:weight ratios indicated the eggs were at similar stages of incubation. When examined for fertility on 26 July, one of the three whole eggs contained a 30 mm long embryo. The contents of the other two eggs had putrefied and no signs of embryonic development could be detected.

Nests with more than two eggs have been rarely documented for the Common Loon. Audubon (Ornithol. Biogr. 4:43–57, 1838) believed three-egg clutches were fairly common, while Bent (U.S. Natl. Mus. Bull. 107:47–62, 1919) thought them to be very rare. Henderson (Condor 26:143–145, 1924) reported two, three-egg clutches in 19 nests from Alberta, and Vermeer (Can. Field-Nat. 87:403–408, 1973) observed one, three-egg clutch in Alberta nests. In contrast, Olson and Marshall (Minn. Mus. Nat. Hist., Occ. Paps. 5:76,1952) recorded
only one- and two-egg clutches from 47 Minnesota nests although they reported "hearing" of a three-egg clutch.

More recently, McIntyre (Ph.D. diss., Univ. Minnesota, Minneapolis, Minnesota, 1975) reported one, three-egg clutch in 51 Minnesota nests. We know of only two reported four-egg loon nests. Peck (pers. comm.) recorded one from Ontario and believed the clutch was laid by two females. Since 1979, information concerning loons has been solicited from the public by the Minnesota Department of Natural Resources (MDNR). Of 76 nests for which clutch-size was reported, one contained three eggs and one contained four (MDNR files).—MICHAEL C. ZICUS, ROSS H. HIER, AND STEPHEN J. MAXSON, Minnesota Dept. Natural Resources, Wetland Wildlife Research Group, 102 23rd St., Bemidji, Minnesota 56601. Accepted 30 Mar. 1983.

Wilson Bull., 95(4), 1983, pp. 672–673


While monitoring approximately 15 loon pairs as part of an intensive nesting survey, I discovered a Common Loon incubating a four-egg clutch on 10 June 1980 on a 22-ha pond inhabited by only one pair of loons. Observations of the pair on open water on 31 May and 7 June indicated incubation had not yet begun. Therefore, the onset of incubation likely occurred between 7 and 10 June. I observed only three eggs on 16 June and one egg on 27 June. The egg remaining on 27 June was cold, indicating the nest had been abandoned.

Several explanations are suggested by these findings. One is that the eggs were laid by different females. This is improbable, however, since the territoriality exhibited by Common Loons would likely prevent another loon from participating in nesting activities. A four-egg clutch could have resulted from a second pair laying eggs in the abandoned nest of another pair. While I never observed more than two loons on the pond during the nesting period, identification of individuals was not possible. Another possibility is that one female laid all four eggs in one breeding cycle. Assuming a laying interval of at least two days (Yonge 1981), this would place the laying of the first egg on or before 4 June, well before the observed
onset of incubation. A final possibility is that an original two-egg nest was abandoned by the loons, and another set of two eggs was laid in the same nest by the same female. The observed onset of incubation is neither early nor late in the season for loons in this area. It is possible, therefore, that the second set of eggs represents a renest attempt. If approximately 14 days elapsed between nest failure and renesting (Sutcliffe 1975), laying of the first clutch probably occurred sometime in late May.

These observations were made while conducting field work for the Loon Preservation Committee of New Hampshire. Appreciation is expressed to Scott Sutcliffe, who reviewed the paper and gave helpful suggestions.—DAVID H. NELSON, Dept. Natural Resources, Cornell Univ., Ithaca, New York 14853. (Present address: Dept. Forestry and Wildlife Management, Univ. Massachusetts, Amherst, Massachusetts 01003.) Accepted 19 Apr. 1983.


Observations suggesting parental division of labor by American Redstarts.—Smith (Can. J. Zool. 56:187–191, 1978) and Nolan (Ornithol. Monogr. No. 26, 1978) have observed parental division of labor during the fledgling period in Song Sparrows (Melospiza melodia) and Prairie Warblers (Dendroica discolor), respectively. However, the generality of parental division of labor is unknown because of the virtual lack of information on the fledgling period in most species. This report describes observations on an American Redstart (Setophaga ruticilla) pair which suggest another example of parental division of labor during the fledgling period.

On 1 August 1981, at the south shore of Bridge Lake (51°29'N, 120°42'W; approx. 80 km N of Kamloops), British Columbia, an adult female redstart was observed feeding one fledged young. About 5 m from the female a male redstart, in first-year plumage, was feeding a second fledgling. A third fledgling was observed sitting quietly on a branch about 1 m from the male. All of the young birds were in complete juvenile plumage as described by Bent (U.S. Natl. Mus. Bull. No. 203, 1953), and their tails appeared to be similar in length to those of the adults. At 17:50 I followed the female for 50 min keeping her and the young she was feeding (YG1) under simultaneous observation. During this time, YG1 followed the female and was fed 15 times by her. The male did not approach or feed YG1, although on three occasions YG1 flew towards the male and begged unsuccessfully.

After observing the female, I followed the male for 20 min and saw it feeding the second fledgling (YG2) once and the third young bird (YG3) twice. While making these observations, the female and YG1 were often seen and their calls were audible. Thus, of the three young birds involved, two associated with one parent and the third with the second parent.

On 2 August, in the same general area, I located what I assume was the same family. The male was observed for 63 min during which it fed two fledglings. During this observation period, the female, who was perched about 8 m up in a tree, remained still; the third young was perched about 2 m below it. I did not observe any begging by this young bird. Once, however, one of the male’s young moved to the same branch as the female and begged directly from the female. The female made no observable response. After the observation period ended, I followed the female for 10 min and saw it feeding the young bird perched below it.

During these observations the male’s two young appeared to take turns being fed. For about 15 min one young actively solicited food while the other perched quietly in shrubbery near the lakeshore. The behavior of the young then reversed. This switching occurred several times during the observation period.

These observations, although anecdotal, suggest a number of interesting things. First,
division of labor by the sexes in feeding the fledglings occurred. Young fed by one parent were not fed by the other, although numerous opportunities existed, and on four occasions young solicited care from the “wrong” adult. I cannot show that stable family units (sensu Nolan 1978; Smith and Merkt, Can. J. Zool. 58:1869–1875, 1980) had been formed because the young birds were not color-marked. However, my four observations of unsuccessful solicitation of food by young from the wrong parent, and the identical number of young tended by parents over 2 days, could be construed as weak evidence for family units.

Finally, these observations suggest that male American Redstarts breeding for the first time can assume a large share of parental care during the fledgling period.

Parental division of labor during the fledgling stage has been documented for the Ovenbird (Seiurus aurocapillus) (Hann, Wilson Bull. 49:145–237, 1937), the Prairie Warbler (Nolan 1978), the Song Sparrow (Smith 1978), and the Eurasian Blackbird (Turdus merula) (Snow, A Study of Blackbirds, George Allen and Unwin, London, England, 1958). In these studies the breeding season was long enough to permit the birds to be double-brooded. Therefore, the division of labor may release the female from feeding all the fledged young in order to lay a second clutch. However, the redstarts in the Bridge Lake area are probably single-brooded. Evidence for this comes from the late migration of this species into the area (mid-to end of May, pers. obs.) and the closeness of the beginning of the fall migratory period at the time these observations took place. Using 19–20 days as the period of incubation and nesting stages combined (Sturm, Auk 62:189–206, 1945), and assuming the redstart’s fledgling period is similar in duration to that of Prairie Warblers (approx. 30 days, Nolan [1978]), the fledglings observed were about 40 days old. Thus, they were likely the first and only successful brood.

Division of labor by birds with a very short breeding season may facilitate the production of a single brood during a period when prebasic molt and other physiological preparations must occur prior to migration.

Acknowledgments.—I thank J. N. M. Smith, V. Nolan Jr., M. Ficken, and G. Holton for their comments on this manuscript.—Peter C. Boxall, Fish and Wildlife Division, Energy and Natural Resources, South Tower, Petroleum Plaza, 9915-108 St., Edmonton, Alberta T5K 2C9, Canada. Accepted 12 Apr. 1983.


Violation of ideal nest placement: Cliff Swallows entombed by their own excrement.—Cliff Swallows (Hirundo pyrrhonota) construct globular mud nests with entrance tubes pointing downwards. Nests are constructed under overhanging cliff ledges or man-made structures, often touching one another. Nest placement by Cliff Swallows approaches the hexagonal, maximum density packing pattern (e.g., see Enlen, Auk 71:16–35, 1954, plate 5 for good photographs; Barlow, Anim. Behav. 22:876–878, 1974). The hexagonal pattern confers several advantages to the builders. Both the strength of the nest and the inside volume are maximized relative to the quantity of mud used in nest construction. Since the first nests to be built in a colony are generally placed in a horizontal row (Enlen 1954, pers. obs.), subsequent nests built below should be diagonally offset relative to those above. Violations of this last principle are infrequent, particularly on the regular surfaces afforded by man-made structures, but they do occur on occasion.

Observations were made in a 50-pair Cliff Swallow colony located beneath a concrete irrigation structure in north-central Washington during the months of June and July 1982. My attention was called to a pair of nests, one built directly beneath the other instead of offset to one side as usual. Ordinarily, Cliff Swallow nestlings defecate out the nest hole and
the feces fall free to the ground. In this case, however, the lower nest protruded beyond the upper nest and accumulated a hard layer of urate left by droppings from above. By the time the chicks in the upper nest were 18 days old, their accumulated excrement had partially obstructed their own nest opening. The parents were apparently no longer able to enter the upper nest although they continued feeding their chicks through the opening as usual. At 23 days, the mature chicks tried to leave the nest but were able to fit only their heads through the reduced opening, a semicircle of 2-cm radius. The brood in the lower nest fledged normally.

The following day, parental feeding had ceased at the upper nest so I chipped away the solidified guano and freed the young. All four chicks were of normal weight and wing length; however, one had died the previous day. The three live chicks had dried excrement on their throat feathers but flew away readily. Without my intervention the remaining chicks presumably would have died shortly.

Suboptimal nest placement often confers fitness costs to the builders, directly through early nest collapse or indirectly through the energetic costs of collecting extra mud. The surprising result of this incident was the much greater cost to the pair nesting above. Although this outcome was predictable to human observers when the nestlings were only half grown, the parent swallows made no attempt to renest, extend the existing entrance tube, or scrape away the accumulating guano. I can only guess that this problem is sufficiently new, i.e., a side effect of nesting on man-made structures, or rare, that selection has been insufficient to render a solution.—PHILIP K. STODDARD, Animal Behavior Program, Psychology Dept., NI-25, Univ. Washington, Seattle, Washington 98195. Accepted 15 Feb. 1983.

Wilson Bull., 95(4), 1983, pp. 675–682


The objective of this study was to quantitatively describe courtship behavior of dabbling ducks during autumn and winter. Emphasis was placed on determining chronology of pair bond formation, estimating proportion of time allocated to reproductive behavior and describing the pattern of courtship activity.

Study area and methods.—The study was conducted from October through February in 1978–79 and 1979–80 on Bodie Island, part of the Cape Hatteras National Seashore, Dare Co., North Carolina. Six species were studied: Gadwall (Anas strepera), Black Duck, American Wigeon (A. americana), Northern Shoveler (A. clypeata), Pintail (A. acuta), and Green-winged Teal (A. crecca carolinensis).

Data on reproductive behavior were compiled using both focal individual and ad libitum sampling (Altmann, Behaviour 49:227–265, 1974). With focal individual sampling, we attempted to observe each species once during each hour from sunrise to sunset every month from November through February. During 1-h sample periods, 10 focal individuals were selected and observed for 5 min each. Observations of behavior were recorded continuously with a cassette tape recorder. Each sample provided a record of the frequency of all behav-


Table 1

Mean (±SE) Percent Time Allocated to Reproductive Behavior, 1978-79 and 1979-80

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<tr>
<td>Gadwall</td>
<td>17.0 (0.8)</td>
<td>19.2 (0.5)</td>
<td>15.8 (0.2)</td>
<td>15.8 (0.04)</td>
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<td>13.3 (0.9)</td>
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<td>Wigeon</td>
<td>18.3 (0.4)</td>
<td>11.2 (0.8)</td>
<td>6.4 (0.5)</td>
<td>—  (NS)</td>
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<tr>
<td>Shoveler</td>
<td>16.7 (0.0)</td>
<td>18.7 (0.1)</td>
<td>15.1 (0.2)</td>
<td>13.3 (0.6)</td>
<td>NS</td>
</tr>
<tr>
<td>Pintail</td>
<td>16.7 (0.0)</td>
<td>18.7 (0.2)</td>
<td>15.8 (1.1)</td>
<td>11.7 (0.8)</td>
<td>&lt;0.01</td>
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<tr>
<td>Green-winged Teal</td>
<td>19.2 (0.0)</td>
<td>19.2 (0.4)</td>
<td>15.0 (1.6)</td>
<td>15.8 (0.6)</td>
<td>&lt;0.001</td>
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</tbody>
</table>

*ANOVA on rank transformed data.

**Total hours of observation using focal individual sampling.

Behaviors, including reproductive behaviors, and time spent performing each. Ad lib sampling was used during periods when focal samples were not employed and aided the overall description of courtship activity. Observations in October consisted entirely of ad lib samples, but this sampling technique was used secondarily in other months.

Classification of reproductive behaviors follows previous studies (Lorenz, Avic. Mag. 57, 58, 59, 1951-1953; Johnsgard 1960; Johnsgard, Handbook of Waterfowl Behavior, Cornell Univ. Press, Ithaca, New York, 1965; McKinney, Wilson Bull. 77:112-121, 1965; Smith, Auk 85:381-396, 1968; McKinney, Living Bird 9:29-64, 1970) with the following exceptions: (1) all displays that involved preening ("preen-behind-the-wing," "preen dorsally," and "belly preen") were placed under the general heading "preening": (2) displays of "head shake," "head flick," "tail wag," "bill dip," "drink," and "wing flap" were assembled under the heading "maintenance": and (3) all displays involving copulatory behavior (pre- and postcopulatory displays) were placed under "copulatory behavior." "Swimming" by individuals within courting groups was considered reproductive behavior. Birds used swimming primarily to position themselves for display, and a more accurate estimate of time allocated to reproductive activity was obtained by including it.

To estimate pairing chronology, a random sample of females from each species was selected monthly and the proportion of paired females was determined. Several criteria were used to determine pair status. The best criterion was sustained proximity to a member of the opposite sex, but other behaviors, such as female "inciting," following of a particular male by a female, and male defense of the female were also used as indicators of pair bond formation. Females were observed for 5 min before assessing and recording pair status.

Percent time allocated to reproductive behavior was calculated for 1-h sample periods and mean percents tabulated for each month. Yearly estimates were combined for analysis. Statistical analysis of percent time spent in reproductive behavior was performed using

Results.—Data are based on 354.5 h of focal individual sampling. Proportion of time allocated to reproductive behavior varied significantly among months for Gadwall, Green-winged Teal, and Pintail but not for the other species (Table 1). Proportion of time spent each month in reproductive behavior did not differ significantly ($P > 0.05$) by sex for any species.

Gadwall.—Courtship activity for Gadwalls was observed initially in late October, but displays performed suggested that courtship began earlier. For instance, females incited and were aggressive to single males, indicating that females in early courting groups were paired. Males performed a wide range of displays including “burp,” “introductory shake,” “grunt-whistle,” and “head-up-tail-up turn-to-female” (HUTU-TTF). HUTU-TTF is characteristic of courtship activity of intermediate intensity (Johnsgard 1960). Gadwalls also engaged in “courtship flights,” and based on our observations of other species, this behavior usually occurred late in the pairing process as competition among males intensified.

Proportion of time spent in reproductive behavior was greatest in November and decreased thereafter (Table 1). In November, males performed burping most frequently and inciting was the most frequent of female displays (Table 2). “Jump flights” and aggression among courting males were also common. Approximately 92% of female Gadwalls had formed pair bonds in November (Table 3). Copulation occurred initially on 9 November.

In late winter, time spent in reproductive behavior decreased, but intensity of courtship remained high as courtship was initiated primarily by unpaired males. Although copulations were not recorded during focal samples in late winter, copulatory behavior by paired individuals was not uncommon at this time and probably served to strengthen pair bonds (see Johnsgard 1960).

Black Duck.—Black Ducks participated in courtship behavior in early October. Males displayed to females with grunt-whistle, HUTU-TTF and “nodswimming” and females were
observed inciting and nodswimming. Paired individuals were common in October, indicating that courtship activity commenced sometime before our observations.

Proportion of time spent in courtship did not change significantly from November through February (Table 1). In November, males performed displays of every intensity and inciting was performed regularly by females in courting groups (Table 4). Copulatory behavior also was recorded. Approximately 97% of females were paired in November (Table 3). Black Ducks initiated courtship and began pairing earlier than any other species studied.

Intensity of courtship remained high throughout December, January, and February. Pair bonds were stable, however, and single males were never successful in breaking up pairs.

Wigeon.—In late October, male Wigeon in alternate plumage displayed with burps, “folded-wings-raised-high-overhead” (FWRHO), and jump flights. Some females in courtship groups incited, so formation of pair bonds had begun. Even though reproductive behavior was not common at this time, displays performed suggested that courtship activity was initiated previous to our observations.

Proportion of time spent in courtship did not change significantly by month (Table 1). In November, courtship activity frequently was characterized by aggression among males. Females displayed with “chinlifting” and inciting, and common male displays were maintenance (8.3%), preening (6.2%), introductory shake (2.1%), and FWRHO (2.1%). Approximately 84% of females were paired in November (Table 3). In December, males performed burping (33.3%) most frequently, followed by maintenance (12.8%) and FWRHO (7.3%); females primarily incited. Jump flights were also common in December (4.0%). In January, females principally incited and the most common male displays were preening (18.7%), maintenance (11.6%), and FWRHO (3.1%). Gradual dispersal of individuals from the study area made it impossible to obtain a full record of courtship throughout winter.

Shoveler.—Reproductive behavior by Shovelers was rarely observed during periods of focal

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### Table 3

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<td>70.6</td>
<td>84.6</td>
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<td>N = 45</td>
<td>N = 45</td>
<td>N = 30</td>
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<td>9.0</td>
<td>84.4</td>
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<tr>
<td>Green-winged Teal</td>
<td>N = 49</td>
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<td>N = 41</td>
<td>N = 44</td>
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<tr>
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<td>2.0</td>
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<td>31.7</td>
<td>79.5</td>
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individual sampling (Table 1); however, ad lib sampling greatly aided description of pairing activity. Only males in alternate plumage displayed to females. In early November 6% (N = 36) of males were in alternate plumage and no courtship was recorded during this month (Table 1). Some females were paired in November (Table 3); however, because courtship was rarely observed, development of these associations was unclear.

Courtship groups occurred initially in early December. Aggression among courting males was infrequent and male displays consisted of jump flight and “head dip.” Intensity of courtship was low and groups soon dispersed. Courtship activity became more frequent in late December. Most males were in alternate plumage and displayed most frequently with jump flights. In January, jump flights remained the most prevalent male display and aggression among males in courtship groups was frequent. Approximately 66% of females were paired in January. Copulatory behavior occurred initially on 17 January, and all major displays described by McKinney (1970) had been observed by the end of the month. In February, over 95% of females were paired. Pair bonds were stable and attempts made by unpaired males to disturb established pair bonds were unsuccessful.

**Pintail.**—Most males attained alternate plumage in mid-November and initiated courtship by swimming up to females and burping. Females showed no interest in these males and continued their regular activities; males soon dispersed. Reproductive activity occurred in ad lib sampling but courtship was not recorded in focal samples during November. No females were paired in November (Table 3).

Pintail courtship activity continued at low frequency and intensity into December. Males circled females while burping; females usually showed no interest and males stopped displaying. In the second week, courtship behavior was still infrequent but it intensified as burp, grunt-whistle, and HUTU-TTF displays were performed by males. Nodswimming was the most common female display (Table 5). Courtship behavior became more frequent in

### Table 4

PERCENT TIME SPENT IN REPRODUCTIVE BEHAVIORS AND DISPLAYS BY MALE AND FEMALE BLACK DUCKS WINTERING AT BODIE ISLAND, NORTH CAROLINA

<table>
<thead>
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<tbody>
<tr>
<td></td>
<td>M</td>
<td>F</td>
<td>M</td>
<td>F</td>
</tr>
<tr>
<td>Swimming</td>
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<td>44.1</td>
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<tr>
<td>Burp</td>
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<tr>
<td>Introductory shake</td>
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<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>Grunt-whistle</td>
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<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>HUTU-TTF</td>
<td>1.2</td>
<td>—</td>
<td>0.0</td>
<td>—</td>
</tr>
<tr>
<td>Down up</td>
<td>1.8</td>
<td>—</td>
<td>0.0</td>
<td>—</td>
</tr>
<tr>
<td>Nodswimming</td>
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</tr>
<tr>
<td>Maintenance</td>
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<td>0.0</td>
</tr>
<tr>
<td>Jump flight</td>
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<td>0.0</td>
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<td>Inciting</td>
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<td>26.8</td>
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<tr>
<td>Copulatory behavior</td>
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<td>3.8</td>
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<tr>
<td>Total&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.4</td>
<td>10.6</td>
<td>2.3</td>
<td>2.2</td>
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</tbody>
</table>

<sup>a</sup>Time observed (min).

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**NOTES**

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late December. Low intensity displays still were most common for both sexes, but some females were observed inciting, indicating pair bonds were beginning to form.

Proportion of time spent in reproductive behavior was greatest in January (Table 1). Males used displays of every intensity, and females were inciting more often and nodswimming less (Table 5). High intensity behaviors such as jump flights and copulatory behavior were performed. Approximately 85% of females were paired in January (Table 3).

Proportion of time spent in courtship decreased in February. During this period, courtship was initiated by unpaired males. If approached by unpaired males, paired males usually attempted to lead the female away as she incited but they sometimes also attacked the intruding males.

Green-winged Teal.—Courtship activity by Green-winged Teal was observed first in November during ad lib sampling but did not occur in focal samples until December. In November, males in alternate plumage displayed with low intensity burps and grunt-whistles only after they had been excited in some manner.

Courtship activity increased in December, but intensity and frequency of courtship behavior in this month varied during the two years of study. In 1978, intensity of courtship increased during the first week of December. Male courtship consisted of low and intermediate intensity displays (burp, grunt-whistle, and HUTU-TTF) while females performed nodswimming and maintenance displays. Courtship flights were observed in the second week of December and more intense reproductive activity continued throughout the month. Few females had paired by the end of December.

In contrast, reproductive activity was infrequent throughout December 1979. Reproductive behavior was observed only after birds had been excited and consisted of burps and grunt-whistles. Individuals displayed briefly and soon dispersed. Like the previous year, few females had formed pair bonds by the end of the month (Table 3).

<table>
<thead>
<tr>
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<td>Swimming</td>
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<tr>
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<td>17.2</td>
<td>—</td>
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<td>—</td>
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<tr>
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<td>—</td>
<td>1.5</td>
<td>—</td>
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</tr>
<tr>
<td>Grunt-whistle</td>
<td>0.0</td>
<td>—</td>
<td>1.0</td>
<td>—</td>
<td>0.0</td>
<td>—</td>
</tr>
<tr>
<td>HUTU-TTF</td>
<td>0.0</td>
<td>—</td>
<td>0.5</td>
<td>—</td>
<td>0.0</td>
<td>—</td>
</tr>
<tr>
<td>Down up</td>
<td>0.0</td>
<td>—</td>
<td>0.0</td>
<td>—</td>
<td>0.9</td>
<td>—</td>
</tr>
<tr>
<td>Nodswimming</td>
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<td>2.9</td>
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<td>0.0</td>
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<tr>
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<td>1.5</td>
<td>0.0</td>
<td>0.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Maintenance</td>
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<td>10.0</td>
<td>2.5</td>
<td>13.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Jump flight</td>
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<td>6.4</td>
<td>0.5</td>
<td>0.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Inciting</td>
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<td>—</td>
<td>34.9</td>
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<td>50.0</td>
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<tr>
<td>Copulatory behavior</td>
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<td>0.0</td>
<td>4.4</td>
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<td>0.0</td>
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<tr>
<td>Totala</td>
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<td>1.8</td>
<td>16.9</td>
<td>8.6</td>
<td>9.6</td>
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</table>

* Time observed (min).
In both years, proportion of time spent in reproductive behavior by Green-winged Teal was greatest during January (Table 1). Aggression was common among males in courtship parties. Males performed displays of every intensity, including high intensity "down-up" and "bridling" while inciting was performed initially by females (Table 6). During January approximately 32% of females were paired. Copulatory behavior occurred during January in 1979 but not in 1980. In February, proportion of time spent in reproductive activity decreased (Table 1), but intensity of courtship remained high. Proportion of paired females increased in February, and by early March approximately 80% of female Green-winged Teal were paired.

Discussion.—This study is the first to quantify and compare reproductive behavior of several species of waterfowl during winter at a single location. Considerable variation in timing of courtship activity occurred among species. Initiation of reproductive behavior was related closely to attainment of alternate plumage. Species which developed alternate plumage late (e.g., Green-winged Teal, Pintail) began courtship later and paired later. Weller (1965) also concluded that chronology of courtship activity and eventual pair bond formation in the genus Aythya was closely linked to development of alternate plumage. This same trend has been reported for other species of waterfowl as well (McKinney 1970, Arntbruster 1982).

A general pattern of reproductive behavior occurred in wintering dabbling ducks from initiation of the pairing process until most females were paired. At first, courtship activity was infrequent and males performed displays of low intensity (e.g., burp, grunt-whistle, introductory shake). Females often were not receptive to early courtship attempts, and this lack of receptivity seemed to deter and shorten male display. In addition, few aggressive interactions among courting males were observed. As pairing continued, courtship activity
increased in intensity. Courtship at this time frequently was characterized by aggression among males, courtship flights, jump flights, and copulatory behavior. In addition, males performed a greater diversity of displays, and females displayed most often by inciting. Reproductive behavior continued at this high level until most females had paired. At this time, frequency of courtship usually declined but intensity of display remained unchanged. Late in the pairing process, attempts by single males to disrupt established pair bonds were never successful.

Acknowledgments.—We thank the National Park Service, especially C. Gifford, for providing access to the Cape Hatteras National Seashore. Financial support was provided by the N.C. Agricultural Experiment Station, the N.C. Wildlife Resources Commission, and the National Wildlife Federation. We also thank P. D. Doerr, R. A. Lanci, and J. R. Walters for reviewing the manuscript. This is paper 8454 of the Journal Series of the N.C. Agricultural Research Service, Raleigh, North Carolina 27650.—GARY R. HEPP AND JAY D. HAIR, Dept. Zoology, P.O. Box 5577, North Carolina State Univ., Raleigh, North Carolina 27650. (Present address JDH: National Wildl. Federation, 1412 16th Street, NW, Washington, D.C. 20036.) Accepted 22 Feb. 1983.


Expectable decline of forest bird populations in severe and mild winters.—In an earlier paper (Graber and Graber, Wilson Bull. 91:88–103, 1979) we described the change of bird numbers in three habitats in southern Illinois between early winter (26 December–7 January) and late winter (3–18 February) during 1976–77, an especially cold winter with heavy snow. On average, bird populations that season declined about 58% in mature bottomland forest, and 66% in mature upland forest, but increased slightly (9%) in urban residential habitat. We attributed the change to mortality and local movements of birds. Those observations posed two other questions of interest to us: (1) How would populations vary in a mild winter? and (2) Is there a predictable rate of change during the winter season?—important questions for those who census birds.

Methods.—To find the answers we censused, using the same methods on some of the same areas, early (26 December–11 January) and late (25 January–15 February) winter in 1977–78 (another severe winter) and 1979–80 (a mild winter). The relative severity of those winters is indicated in Table 1. Our attempts to acquire data early and late in the winters of 1978–79 and 1981–82 were frustrated by floods and ice storms. Within the seasonal limits posed by the study, we censused every day that weather permitted. The periods of censusing were chosen to avoid early and late migration. We varied coverage of habitats in the different years to consider different problems concerned with the census. In 1977–78, to consider population variability, we censused seven bottomland forest areas (Nos. 1, 2, 6, 8, 10, and two forests at No. 11 in Fig. 1 of Graber and Graber [1979]). The variability shown (Table 2) includes variation from the census method and from the habitats as well as the populations. For that reason and because of the small number of areas that could be censused in the time available, the standard errors are large. Differences between early winter and late winter populations (all native species) in the seven bottomland forest areas were significant ($t = 2.72, df = 12, P < 0.02$).

Because it is important to know whether decline in numbers of birds represents mortality or movement to other habitats, we censused representative areas of the principal arboreal habitats in southern and central Illinois. In the mild winter of 1979–80 (Table 3), in addition to mature bottomland (No. 10 in Fig. 1 of Graber and Graber [1979]) and mature upland forest (Warbluff Forest, 10 km N, Golconda, Pope County), we censused upland forest-edge
and shrub habitat, and 40-year-old loblolly pine (Pinus taeda) plantation habitat, both in the Warbluff area. In east-central Illinois we censused mature bottomland forest, mature upland forest, and forest-edge and shrub habitat, all in Allerton Park, Piatt County. The southern Illinois forests were described in the earlier paper. In central Illinois tree genera of the upland forest, listed in order of importance, were Quercus, Carya, Ulmus, Acer, and Fraxinus (comprising 85% of the Importance, Y). The bottomland forest consisted of Acer, Celtis, Platanus, Fraxinus, Carva, Quercus, and Ulmus (85% of Y). Each tract was censused twice in early winter and twice in late winter. As expected, variability was high, but differences between the early censuses in all tracts were not significant (t = 0.02, df = 12, P > 0.90), nor were those between the late censuses (t = 0.14, df = 12, P > 0.80). On that basis, the early pairs were combined and the late pairs, combined in Table 3. In all habitats, central and south, bird populations declined between the early and late winter counts (Table 3). Because censuses in the different areas were necessarily made on different dates, the periods between early and late censuses varied somewhat from habitat to habitat, and year-to-year. Therefore, in the text we have usually referred to population changes as average percentage change per day. Because we censused more areas of bottomland forest than of other habitats, the following discussion primarily concerns bottomland.

To save space, only the most common native species are listed in Tables 2 and 3, but the densities for all native species combined (excluding Cedar Waxwing [Bombycilla cedrorum]) are provided. The waxwing was excluded as the only native species present in early winter that always disappeared by late winter. Its inclusion would have accentuated the difference between early and late winter densities. The Eurasian Starling exhibited somewhat the same pattern. It disappeared from natural habitats between early and late winter (as in 1976–77) but increased greatly in urban habitat by late winter (Table 2).

Results and discussion.—A pattern of population change observed in both the severe winters of 1976–77 and 1977–78 was that the steepness of the decline was related to the size of the early winter populations (Fig. 1). There were significant correlations between the early winter population and the population loss per day during the severe winters (1976–77, r = 0.83, F = 6.58, df = 3, 5, P < 0.05; 1977–78, r = 0.79, F = 8.52, df = 5, 7, P < 0.01). The slopes of the regression lines were not significantly different in the 2 years. The decline of populations in bottomland forests during both severe winters can be expressed by the equation: \( P_d = D_i (0.00267) \), in which \( P_d \) is the average percent loss in population per day during the period covered by the censuses, and \( D_i \) is the initial population density (birds/40.5 ha). The equation may not apply to upland forests, which start (and end) the winter with generally lower populations, but we have insufficient censuses of upland areas or other habitats to test the equation. The end-of-winter densities in bottomland tend to converge at

<table>
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<tr>
<th>Season</th>
<th>Decatur DD</th>
<th>Days with snow cover</th>
<th>Avg. snow depth (cm)</th>
<th>Dixon Springs DD</th>
<th>Days with snow cover</th>
<th>Avg. snow depth (cm)</th>
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<td>33</td>
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<tr>
<td>1977–78</td>
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<td>8.3</td>
<td>−232.5</td>
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<td>13.6</td>
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<td>1979–80</td>
<td>−146.9</td>
<td>14</td>
<td>2.4</td>
<td>−7.2</td>
<td>14</td>
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### Table 2

**Changes in Numbers of Winter Birds per 40.5 ha in Arboreal Habitats in Southern Illinois during a Severe Winter (1977–78)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Bottomland forest</th>
<th>Upland forest</th>
<th>Urban residential</th>
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<tbody>
<tr>
<td></td>
<td>Early $\bar{x}$ ± SE</td>
<td>Late $\bar{x}$ ± SE</td>
<td>% Change</td>
</tr>
<tr>
<td>Yellow-shafted Flicker</td>
<td>5.2 ± 1.38</td>
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<tr>
<td>(Colaptes auratus auratus)</td>
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<tr>
<td>Red-bellied Woodpecker</td>
<td>7.1 ± 2.33</td>
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<tr>
<td>(Melanerpes carolinus)</td>
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<td></td>
</tr>
<tr>
<td>Red-headed Woodpecker</td>
<td>78.6 ± 12.33</td>
<td>74.6 ± 15.12</td>
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<tr>
<td>(M. erythrocephalus)</td>
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<td></td>
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<tr>
<td>Downy Woodpecker</td>
<td>15.1 ± 4.00</td>
<td>11.7 ± 3.61</td>
<td>-22</td>
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<tr>
<td>(Picoide pubescens)</td>
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<td></td>
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<tr>
<td>Blue Jay</td>
<td>16.7 ± 6.34</td>
<td>7.9 ± 2.02</td>
<td>-53</td>
</tr>
<tr>
<td>(Gymnocitta cristata)</td>
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<td></td>
<td></td>
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<tr>
<td>Carolina Chickadee</td>
<td>10.6 ± 4.30</td>
<td>14.1 ± 5.14</td>
<td>+33</td>
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<tr>
<td>(Parus carolinensis)</td>
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<tr>
<td>Tufted Titmouse</td>
<td>23.8 ± 4.22</td>
<td>11.7 ± 3.16</td>
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<td>(P. b. bicolor)</td>
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<tr>
<td>White-breasted Nuthatch</td>
<td>3.9 ± 1.97</td>
<td>2.4 ± 1.14</td>
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<tr>
<td>(Sitta carolinensis)</td>
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<tr>
<td>Brown Creeper</td>
<td>1.6 ± 0.66</td>
<td>6.2 ± 1.86</td>
<td>+287</td>
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<td>(Certhia familiaris)</td>
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<tr>
<td>Golden-crowned Kinglet</td>
<td>0.6 ± 0.64</td>
<td>0.3 ± 0.30</td>
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<td>(Regulus satrapa)</td>
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<td>Ruby-crowned Kinglet</td>
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<td>(R. calendula)</td>
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<td>Yellow-rumped Warbler</td>
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<td>Species</td>
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<td>-----------------------------</td>
<td>------------------------</td>
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<td>Early</td>
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<tr>
<td>(Cardinalis cardinalis)</td>
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<td>± 1.25</td>
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<td>Dark-eyed Junco</td>
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<td>-80</td>
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<td>(Junco hyemalis)</td>
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<td>All native birds</td>
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<td>(Columbia livia)</td>
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<tr>
<td>Eurasian Starling</td>
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<td>(Sturnus vulgaris)</td>
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Population densities of forest birds in early and late winter in seven bottomland forest areas in southern Illinois. Numerals indicate localities (see Wilson Bull. 91:89, 1979, for identifications). Nos. 11 and 11A are two forests in the same general area. Data refer to the severe winter of 1977-78 except where otherwise indicated.

A population level of about 150–200 birds/40.5 ha (Fig. 1), presumably the ultimate carrying capacity of the particular forest for the season.

The severity of the winter undoubtedly influences the rate of decline; 1976–77 and 1977–78 were about comparable in measurable factors of severity (Table 1), and rates of decline

---

Fig. 1. Population densities of forest birds in early and late winter in seven bottomland forest areas in southern Illinois. Numerals indicate localities (see Wilson Bull. 91:89, 1979, for identifications). Nos. 11 and 11A are two forests in the same general area. Data refer to the severe winter of 1977-78 except where otherwise indicated.
were similar in the two. In the mild winter of 1979–80 we censused only one bottomland forest (Heron Pond Nature Preserve) in which bird populations had a rate of decline during the winter of 1.16%/day, vs 1.85%/day in the severe winter (Fig. 1), even though the initial density was higher in the mild winter. Thus, we would not expect the equation for rate of decline to fit in a mild winter. Data for Wood Pigeon (*Columba palumba*) and Coal Tit (*Parus ater*) populations in England showed the same pattern of steep decline in severe winters, and less steep decline in mild winters (Lack, Population Studies of Birds, Clarendon Press, Oxford, England, 1966:88, 183) that we have seen in Illinois. It was not possible to determine precise rates of change for the England data, as the specific starting and ending dates of the studies were not stated.

The precision with which the initial population seems to predict rate of decline is somewhat surprising, as food resources (and other factors) could be expected to be an important factor bearing on population change during the winter. However, the direct influence of the food resources could be concealed if the initial population itself reflects the available food.

Though the slope of decline was less in a mild winter, it was still substantial (Table 3, Fig. 1). What caused the decline? A significant feature of the over-winter change in bird populations was its consistent trend in all forest habitats and nearly all forest species in both central and southern Illinois (Tables 2, 3). Major potential means by which winter population in an area may change significantly—local movement, migration, and mortality—may all be involved in the decline we observed. The only habitat that has consistently shown population increase by later winter was urban residential, a habitat, which though now rapidly expanding, accounts for only about 13% of arboreal habitat area in southern Illinois (Graber and Graber, III. Nat. Hist. Surv. Biol. Notes 97:6, 1976). Urban residential habitat would account for no more than 15% of the birds lost from natural habitats, based on data in Tables 2 and 3.

Little appears to be known about winter migration. Of the forest species we observed, only the Black-capped Chickadee is known to undertake (irregularly) winter migrations (DeSante, Am. Birds 30:679, 1976). In both severe and mild winters only two “species”—chickadees (at least Black-capped) and Brown Creeper—increased during the winter in natural habitats. Reference in Tables 2 and 3 to Carolina Chickadees (only) in extreme southern Illinois is based on the fact that we have rarely identified black-caps that far south in the state. It is possible that some of the chickadees we counted were actually black-caps, and that the observed increase in chickadees represented immigration. Winter migration of Brown creepers has not been substantiated so far as we know, but our data indicate that such migrations occur.

Of the factors that could explain the observed general decline of birds during winter, we consider mortality to be most important. The observed rate was not necessarily above expected mortality. Annual mortality rates for adult song birds have been estimated from banding studies of different species and in different years to be 37–67% or 0.10–0.18%/day (Farner, Wilson Bull. 57:63, 1945; Hickey, U.S. Fish and Wildl. Serv. Spec. Sci. Rept. 15, 1952; Nice, Studies in the Life History of the Song Sparrow, Vol. 1, Dover Publications, New York, New York, 1964). Overwinter mortality of banded adult Song Sparrows was 14.26% (Nice 1964), and of adult Black-capped Chickadees, 10% or less to 20% in different years (Wallace, Bird-Banding 12:62–63, 1941). The high extremes in these banding studies approach or exceed the observed declines for a number of species on our study areas (Table 3). The winter declines we observed refer to a particular segment of any such populations (e.g., those that winter in the mid-temperate latitudes). Perhaps more importantly, the observed decline starts with the population of birds at a relatively high point in its annual cycle. Thus, the effect of a 1% per day average mortality could still leave the population at the end
<table>
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<th>Region</th>
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<th>Upland forest</th>
<th>Upland forest edge and shrub</th>
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<td>104.2 41.8</td>
<td>226.9b 137.0</td>
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<td>37.1 36.9</td>
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<td>-34.3 34.1</td>
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* Dates of censuses.
* Excludes Cedar Waxwings.
of winter above that in the preceding spring, depending upon over-all productivity, mortality in other habitats and wintering areas, and other factors.

It is impossible for a single team of observers to adequately census all habitats in a region within the time limitations required, but studies that do not cover all of the habitats used by the winter species are likely to be misleading on questions of population change during the season. Habitat availability must also be considered in such studies, but data on availability of even gross (vs micro) habitat types are generally lacking. Two patterns that seem clear from this and our previous (1979) study is that notable declines occur over winter in natural habitats in mild as well as in severe winters, and that the steepness of the decline is related especially to the size of the starting population.

The observation that bird populations declined through the winter in both mild and severe winters is important to those who census winter birds. The seasonal limits designated for Audubon winter bird studies is 20 December–10 February (Robbins, Studies in Avian Biology 6:52–57. 1981). The results would differ according to the pattern of censusing in that period—early censuses indicating high populations, later censuses lower populations. Fortunately the dates of censuses are usually presented, but the rules of censusing may need to be more precisely delineated, as Robbins (1981) has suggested.

Acknowledgments.—We are indebted to Richard E. Warner and Glen C. Sanderson of the Illinois Natural History Survey for helpful suggestions on the original manuscript.—JEAN W. GRABER AND RICHARD R. GRABER, Illinois Natural History Survey, Natural Resources Bldg., 607 E. Peabody, Champaign, Illinois 61820. Accepted 9 Feb. 1983.

Wilson Bull., 95(4), 1983, pp. 690–694

Comparative preening behavior of wild-caught Canada Geese and Mallards.—Comfort movements have been described for many birds (c.f., Goodwin, Br. Birds 60:363–364, 1967; Weisbrod, Living Bird 10:271–284, 1971; Ainley, Behaviour 50:16–51, 1974; Potter and Hauser, Auk 91:537–563, 1974). Preening, perhaps the most conspicuous of all comfort movements, functions in cleaning, arranging, aligning, and oiling the feathers.

Preening is usually observed in bouts lasting from a few minutes (Coutlee, Wilson Bull. 75:342–357, 1963) to over 2 h (Schreiber, Ornithol. Monogr. No. 22. 1977). McKinney (Behaviour 25:120–220, 1965) divided preening bouts in waterfowl into two main components, oiling and nibbling. Oiling is characterized by contact with the uropygial gland and the subsequent bill movements which spread oil to the feathers. Nibbling consists of rapid movement of the mandibles in a “chewing” motion.

In this note I report on preening behavior in Canada Geese (Branta canadensis) and Mallards (Anas platyrhynchos) during summer and consider: (1) if there are any general behavioral patterns in a preening session; and (2) possible interspecific differences.

Methods.—This study was conducted at the W.K. Kellogg Bird Sanctuary of Michigan State University. Three-h observation periods were made during daylight hours at randomly chosen times. Observer disturbance was reduced by observing the geese from a distance of 35 m and the Mallards from a blind located 10 m from their pen. To further reduce bias, no data were recorded for the first 30–60 min of each observation period. Usually, only one or two preening sessions were recorded during the 2-h data collection period.

All geese were wing pinioned and housed in six similar outdoor pens (45 × 60 m). Three male and three female geese in each pen were identified by color-coded neck collars. Five male and four female wild-caught mallards were housed in a 8 × 15 m pen located on a small pond.
A session was defined as the time during which preening was observed. Pauses of less than 2 min between subsequent preens were considered part of a session. A preening movement was judged to begin when the bill, head, or foot contacted feathers and to end when contact was broken. Data were recorded from the first bird of a group that began to preen. Although other birds often began to preen at the same time, no data were recorded from them.

Classification of preening (after van Rijn, Behaviour 63:71–109, 1977) was based upon the body area contacted and the form (bill movement and use of the head or foot). The terminology proposed by McKinney (1965) to describe preening movements was used except the term “bill rub” (a movement in which the trailing edge of the bill was brushed against the lay of the feathers) was substituted for the term “oiling.” The body area contacted and form of preening movement was determined. The duration of each movement was reported as a mean for each session, and the table values reported for each response were a mean of the session means. Preening sessions in which oiling occurred were considered to be different from sessions in which it did not. Mann-Whitney U-tests, used for all statistical comparisons, were done at Bowling Green State University.

Results.—Twenty-one oiling and 19 non-oiling sessions which were recorded from Canada Geese contained a total of 2509 preening movements. In Mallards, oiling occurred in 28 of 40 sessions. A total of 2650 preening movements was recorded from Mallards.

Canada Geese preened more during oiling sessions than in non-oiling sessions (87.6 ± 32.6 [± ± SD] vs 37.6 ± 22.8, \(U = 37, N = 19,21, P < 0.001\)). Also, the mean duration of oiling sessions, 16.8 ± 6.9 min, was longer \((U = 98, N = 19,21, P < 0.01)\) than non-oiling. 9.6 ± 5.0 min. Mallard oiling sessions contained more \((U = 71, N = 12,28, P < 0.01)\) preens, 74.9 ± 41.6, than did non-oiling sessions, 46.0 ± 54.6. The average duration of a Mallard oiling session, 10.2 ± 6.5 min, was not significantly greater \((U = 107, N = 12,28, P > 0.05)\) than non-oiling sessions, 7.8 ± 8.3 min.

Nibbles and bill rubs comprised 80% of all preening movements in Canada Geese and Mallards. Nibbles were more frequent \((U = 91, N = 19,21, P < 0.01)\) in Canada Goose oiling sessions (Table 1), while their average durations were not significantly greater \((U = 5, N = 5.5, P > 0.05)\) than in non-oiling sessions. Bill rubs were also more frequent \((U = 7, N = 13,21, P < 0.001)\) in oiling sessions but were not significantly longer \((U = 10, N = 4.5, P > 0.05)\). The bill rub-nibble, a movement combining a bill rub and nibble in rapid succession without feather contact being broken, showed little variation between oiling and non-oiling sessions (frequency: \(U = 38, N = 10.13, P > 0.05\); duration: \(U = 4, N = 2.4, P > 0.05\)). The frequency of bill rubbing in oiling and non-oiling sessions, though significantly different \((U = 46, N = 8.28, P < 0.05)\), was highly variable in Mallards (Table 1). In Mallards, the frequency of hill rubbing per session was found to be bimodally distributed about the mean.

Although the frequency of hill rubbing varied, the average duration was relatively constant \((U = 103, N = 8.28, P > 0.05)\). The other preening movements in Mallard sessions showed only small differences (nibble: frequency \(U = 146, N = 12.28, P > 0.05\); duration \(U = 157, N = 12.28, P > 0.05\); bill rub-nibble: frequency \(U = 37, N = 5.14, P > 0.05\); duration \(U = 21, N = 5.14, P > 0.05\)).

Preening movements involving rubbing of the head on the wings were classified as shoulder-rubbing by McKinney (1965). Shoulder-rubbing was more common in oiling sessions in both species (Canada Geese: \(U = 66, N = 7.21, P > 0.05\); Mallards: \(U = 0, N = 1.28, P > 0.05\)). Canada Geese did not stretch or scratch frequently during preening sessions and no differences were found in frequencies (stretches: \(U = 46, N = 11.7, P > 0.05\); scratches: \(U = 30, N = 6.9, P > 0.05\)) or durations (stretches: \(U = 3, N = 3.2, P > 0.05\); scratches: \(U = 30, N = 6.9, P > 0.05\)).
<table>
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<tr>
<th></th>
<th>Mean frequency of movements (x ± SD) [no. of sessions in which movement was observed]</th>
<th>Mean duration (sec) (x ± SE) [no. of sessions in which movement was timed]</th>
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<tr>
<td></td>
<td>Canada Goose</td>
<td>Mallard</td>
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<tr>
<td>Nibble</td>
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<tr>
<td>Oiling</td>
<td>51.8 ± 26.6 (21)**</td>
<td>42.1 ± 37.7 (28)</td>
</tr>
<tr>
<td>Non-oiling</td>
<td>26.2 ± 18.3 (19)**</td>
<td>31.1 ± 23.7 (12)</td>
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<td>Bill rub</td>
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<tr>
<td>Oiling</td>
<td>16.5 ± 7.8 (21)***</td>
<td>15.7 ± 8.3 (28)*</td>
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<td>Non-oiling</td>
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<td>15.8 ± 31.0 (8)*</td>
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<td>3.4 ± 4.3 (7)</td>
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* Values for oiling and non-oiling having the same number of asterisks are significantly different at the level specified. **P < 0.05, ***P < 0.01, ****P < 0.001.

b Not a mean, but an absolute duration of one observation.
GENERAL NOTES

U = 0, N = 1.1, P \geq 0.05). McKinney (1965) described the both-wing stretch in waterfowl. This movement consists of both wings being raised above the body while the manus remained folded. During my observations I observed only one both-wing stretch in Canada Geese. The duration of only two scratches were recorded from Canada Geese. The occurrence and duration of stretching and scratching movements in Mallard oiling and non-oiling sessions were similar (stretches: frequency U = 27, N = 6.15, \(P \geq 0.05\); duration U = 38, N = 6.15, \(P \geq 0.05\); scratches: frequency U = 60, N = 7.25, \(P \geq 0.05\); duration U = 62, N = 7.25, \(P \geq 0.05\)). Four both-wing stretches were observed in Mallards and lasted 2.5 \pm 0.2 sec.

Comparisons of Canada Goose and Mallard oiling sessions showed that the mean number of movements performed by each species was similar (U = 223, N = 28.21, \(P \geq 0.05\)). However, Canada Geese preened for a longer time (U = 151, N = 28.21, \(P \leq 0.01\)) than Mallards. The frequencies and durations of bill rubs and nibbles were similar for both species (bill rubs: frequency U = 269, N = 28.21, \(P \geq 0.05\); duration U = 42, N = 28.5, \(P \geq 0.05\); nibbles: frequency U = 209, N = 28.21, \(P \geq 0.05\); duration U = 40, N = 28.5, \(P \geq 0.05\)). Although the frequency of shoulder-rubbing was not different (U = 278, N = 28.21, \(P \geq 0.05\)), the duration of shoulder-rubbing was greater (U = 13, N = 28.5, \(P \leq 0.01\)) in Canada Geese.

Stretching and scratching comprised only 4% of all preening movements. No differences were found in the occurrence (U = 50, N = 15.7, \(P \geq 0.05\)) or duration (U = 10, N = 15.2, \(P \geq 0.05\)) of stretching between Canada Geese and Mallards. Scratching movements were more frequent (U = 190, N = 25.9, \(P \leq 0.05\)) in Mallard preening sessions, but there were no differences in the durations of these movements (U = 0, N = 25.1, \(P \geq 0.05\)).

Both Mallards and Canada Geese oiled the same number of times per session (3.3 \pm 1.3 and 3.2 \pm 0.8, respectively; U = 316, N = 28.21, \(P \geq 0.05\)). The duration of gland contact in Canada Geese, 5.8 \pm 0.4 sec, was significantly longer (U = 8, N = 28.5, \(P \leq 0.002\)) than in Mallards, 3.4 \pm 0.4 sec.

Discussion.—Data from the present study on waterfowl and the observations by Bekoff et al. (Wilson Bull 91:255-270, 1979) showed differences between oiling and non-oiling sessions. Non-oiling sessions were shorter and contained fewer preening movements per minute (Table 1). The decrease in duration of non-oiling sessions in both Canada Geese and Mallards can be attributed to the decrease in frequency of bill rubbing and nibbling. The change in frequency of bill rubs and nibbles did not affect the duration of these movements. This further indicated that the differences between oiling and non-oiling sessions were the result of no uropygial gland contact and, therefore, no need to spread preen oil.

McKinney (1965) reported that uropygial gland contact alternates from side-to-side in waterfowl. I also observed this pattern. Both Canada Geese and Mallards preened the same side of the body as that on which the gland was contacted 96% of the time.

Ainley (1974) described a bill movement in penguins associated with uropygial gland contact and similar in form to bill rubs in waterfowl. This movement was first used in a preening session to remove water from the feathers and was termed “wiping” by Ainley. Canada Geese and Mallards performed bill rubs immediately after leaving the water and water droplets were observed being brushed off the feathers.

Because bill rubs occurred in non-oiling preening sessions, and did not perform the sole function of spreading preen oil, the term “oil-” as defined by McKinney (1965), is inappropriate. McKinney’s terminology hinders the description of preening because it forces a function (oiling) on a movement that does not perform that function (wiping or bill rubbing). The use of the term “bill rub” is more appropriate.

Interspecific comparisons of preening showed few differences between Canada Geese and Mallards. McKinney (1965) reported that oiling sessions in Mallards and White-fronted Geese (Anser albifrons) lasted fewer than 5 min. Even though Canada Geese and Mallards contacted...
the uropygial gland an equal number of times per session the duration of contact was longer in Canada Geese.

Acknowledgments.—This paper is based, in part, on a Master’s thesis submitted to the graduate college at Bowling Green State University. I am indebted to Dr. E. Martin for his comments on earlier drafts of the manuscript and his guidance throughout this entire project. Various drafts of this manuscript benefited from the comments of D. Beaver, M. Bekoff, R. Howard, C. MacIlnnes, F. McKinney, R. Romans, and an anonymous reviewer. I would also like to express my thanks to B. LeDonne, P. Vanderploeg, and the staff of the Kellogg Bird Sanctuary for their assistance during this study.—RICHARD A. ROWE, Dept. Biological Sciences, Bowling Green State Univ., Bowling Green, Ohio 43403. (Present address: The Museum and Dept. Zoology, Michigan State Univ., East Lansing, Michigan 48824.) Accepted 15 Apr. 1983.


Bald Eagle predation on domestic sheep.—Bald Eagles (Haliaeetus leucocephalus) feed on domestic sheep (Ovis) (see for example, Retifalvi, Condor 72:358–361, 1970; Platt, Am. Birds 30:783–788, 1976) which, in some areas, may be an important food item during winter (Hancock, Wilson Bull. 76:111–120, 1964). Both carcasses and afterbirths are eaten; but Hancock (1964) reports no incidences of predation by Bald Eagles even though sheep carrion was the eagle’s most prominent food item. Most records of Bald Eagle predation on livestock (e.g., Oberholser, USDA Biol. Surv. Bull. No. 27, 1906; Herrick, Auk 41:389–422, 1924) are circumspect. Only two records (Pirnie, Jack-Pine Warbler 24:105–107, 1946; Wiley and Bolen, Southwestern Nat. 16:151–169, 1971) appear to be authentic, and neither is a first-hand eyewitness account. In both, evidence of eagle predation was based on the presence of characteristic talon punctures accompanied with subcutaneous bleeding (O’Gara, pp. 206–213 in Proc. 8th Vert. Pest Conf., 1978). Even in these cases, Bald Eagles could have displaced a Golden Eagle (Aquila chrysaetos) from a sheep the latter had killed. Sheep and calf predations by Bald Eagles have been reported to us by S. Crowe and B. O’Gara (pers. comm.), but these too are not eyewitness accounts. This note is the first documentation of eyewitnessed observations of Bald Eagles preying on live domestic sheep.

While studying Bald Eagle habitat during the winter of 1980–81 near Woodruff, Rich Co., Utah, we observed Bald Eagles preying on domestic sheep.

At about 11:00 on 10 February 1981 we saw an adult Bald Eagle perched on a fence post 60 m from a band of sheep and 200 m from a ranch house. At 12:50 the eagle flew to and attacked an apparently healthy lamb, estimated to be 4 days old, which was separated from its ewe. The lamb struggled a little, but died shortly. The ewe ran at the eagle once to within 2 m without effect. After about 40 s the eagle flew off, but returned in about 5 min and began to feed while perched on the lamb’s sacral region. At 13:23 the eagle left the carcass, landed in a puddle, wiped its beak, and cleaned its talons.

On 17 February, at 13:12, we observed an adult and an immature Bald Eagle perched near sheep in a pasture 400–500 m from a ranch house. A pregnant ewe had fallen down and was struggling to stand up but could not. Either she simply was unable to stand back up—as sometimes happens with apparently healthy sheep (E. Pearson, pers. comm.)—or she may have been ill. The struggles of the ewe soon attracted the adult eagle which flew from the fence post, landed on the ground, and then jumped on her. The eagle began plucking wool from the sacral area while perched. The ewe continued unsuccessfully to try to stand up. At 13:20 the eagle began to feed in the area it had plucked; it ceased feeding at 13:38 and moving away stood on the ground about 10 m from the ewe. At 13:42 the adult eagle flew
away to bathe and preen in a puddle in an adjacent pasture. At 13:57 it soared upward and then glided out of sight. At 14:05 the immature eagle began to feed on the ewe, but it flushed when we attempted to take photographs. At 14:20 a second adult fed on the still live ewe. At 14:40 a third adult eagle took its turn at feeding. The ewe died overnight. We estimate a total of 4.5 kg of the sheep was consumed by the four eagles; they ate most of one hind leg and parts of ribs and internal organs.

The extent of Bald Eagle predation on domestic sheep in this area of northeastern Utah and southwestern Wyoming is unknown. The scarcity of reliable published accounts suggests that Bald Eagles are not significant predators on domestic sheep. Only in recent years, however, has evidence been gathered to indicate that Golden Eagles may cause serious damage to sheep in certain areas (O'Gara 1978; Crowe, pers. comm.). An increase of Golden Eagle depredations during periods of diminished natural prey has been reported (O'Gara 1978). The amount of predation by Bald Eagles on sheep is likely influenced similarly. During the winter of 1980–81 we noted an abnormally low winter kill of mule deer (*Odocoileus hemionus*), a major food item of wintering Bald Eagles in the Woodruff area. This scarcity of deer carrion may have contributed to the predation on the sheep that we observed.

ORNITHOLOGICAL LITERATURE

THE FALCONS OF THE WORLD. By Tom J. Cade, paintings by R. David Digby. Cornell Univ. Press, Ithaca, New York, 1982:192 pp., 44 color plates, 9 black-and-white drawings, 4 graphs, 5 tables, 31 range maps. $38.50.—Anyone remotely familiar with falcons will recognize the name Tom Cade either for his scientific research or his successful program of breeding Peregrine Falcons (Falco peregrinus) at Cornell University for release into the wild. We are fortunate that he has now chosen to share his vast knowledge of the genus Falco with us in this book. It is one of the few books of its kind that successfully bridges the gap between professional and amateur.

The text is divided into two parts. The first is a general synopsis of Falco dealing with special characteristics of falcons, classification, distribution and migration, size and flying performance, hunting success, reversed sexual dimorphism, social behavior and reproduction, and the relationship between falcons and humans. The second part contains 39 species accounts (the complete genus). For each species general characteristics, distribution, habitat, food, hunting tactics, breeding behavior, population status, and conservation are usually discussed.

Thanks to Cade’s enthusiasm, the text of Part One is both interesting and informative. However, a reader unfamiliar with non-raptorial birds might be led to think that falcons are truly exceptional, when in fact, for many aspects of their biology they are similar to other birds. More comparisons of falcons to other birds, therefore, would have been useful in putting falcon biology in perspective. We are told that a falcon can fly effectively with both alulas missing or damaged, but is this any different than other birds? I would like to have known in what ways falcons are unique.

Many discussions are based on the most recent information available, but some topics and conclusions leave me questioning Cade’s source. An example is the recurrent theme of relative size, shape, and flying performance among falcons. Changes in shape that are the result of increases in size are a mathematically complex problem. Comparisons of size, shape, and flying ability made among species must take allometry into consideration if speculations regarding the ecological adaptation of shape are invoked. I therefore question some of Cade’s comparisons among species, and disapprove of the rather loose manner of referring to relative size. For example, Cade says that insect eaters (kestrels) have relatively smaller and weaker beaks than those falcons like the peregrine that kill difficult quarry. Do they? Using data from Brown and Amadon (Eagles, Hawks and Falcons of the World, Country Life Books, Feltham, Middlesex, United Kingdom, 1968) and White (Biosystematics of the North American Peregrine Falcons, Ph.D. diss., Univ. Utah, Logan, Utah, 1968) my calculations show that the culmen lengths of peregrines (F. p. anatum) and American Kestrels (F. sparverius sparverius) are in exactly the same proportion to the lengths of their respective wing chords (often used as an overall measure of size). If weight is compared to culmen length, then it is the kestrel which has the relatively larger (or at least longer) bill. Such calculations are of little use except to emphasize the problems associated with “size” and “relative.”

Some of the qualitative comparisons made among species are confusing or difficult to understand. For example, the Saker (F. cherrug) is described as a “rough and tumble version” of, and “more rangy in appearance” than, a Gyrfalcon (F. rusticolus). Perhaps the advantages of such a writing style in making the text more interesting, or in conveying an impression of the ecological or behavioral relationships among species, outweigh the disadvantages of such scientific laxity.

Data on wing loadings and other flight-related variables are badly needed for raptors. Cade’s two tables and two graphs on the subject are most welcome, but unfortunately some
hard-to-get data like wing widths are only presented on graphs and hence are not available to other researchers. Species' flight performances are frequently compared in light of their behavior in, and suitability for, falconry, although this is not often explicitly stated. Cade's enthusiastic support for falconry is well illustrated by his description of the peregrine as, "a bird of the gauntlet and the mews just as much as it is a creature of wild river gorges and coastal palisades." Cade emphasizes what he believes is the lack of evidence for falconers having a negative impact on wild populations of falcons. One particularly insightful and lengthy example is that of Arab falconers who harvest about 2000 Sakers per year (about 90% of which are females!).

Cade's passion for falconry is matched only by his concern and conscience for the conservation of all falcons. He presents good reviews of what is known about each species' distribution and biology, and speculates as to their global population status. Some of his numerical estimates may be of limited value, however, because of the dearth of information about some species. For example, we are told that if the Australian Kestrel (F. cenchroides) occurs at the same density as the Common Kestrel (F. tinnunculus) then there could be 75,000-750,000 pairs of cenchroides in existence. The book frequently reminds us that if falcons are to have a future in this world they must do so in coexistence with mankind. Examples of how this is now the case, or how it could be are explored.

Although I have praised Cade's efforts at satisfying both the scientist and amateur alike, there are shortcomings in this regard. The book suffers from the lack of a glossary. Will most non-scientists know what phylogeny or a hallux are? Will non-falconers know what a tiercel, haggard, or passage bird are? Falconry jargon is rampant throughout the book. Furthermore, there are annoying editorial and publication errors. The style of referencing published papers is rather loose; there are inconsistencies and errors between the text and bibliography. Some animals are referred to by both their common and scientific names, while others lack one or the other. The inside of the jacket claims that the book has 40 color paintings and 33 maps. I count 44 paintings (not including the cover) and 31 maps. There is no reason why four maps should each illustrate two species in the same color with no distinguishing labels.

Scientifically speaking, there are three disappointing omissions. Firstly, immature falcons are sadly ignored. There is little information about any aspect of their life history, their plumage is often only very generally described, and some are not depicted in the plates. Secondly, the morphometric data are scant at best, and then often rehashes of measurements from earlier publications. This book could have been far more valuable as a reference text if an appendix of data for as many morphometric characters as available had been included. Thirdly, beyond omitting some immature plumages, the usefulness of plates has been reduced further by not providing the locales from which the specimens used for the paintings came. Also, considering that Cade describes a new color phase of Eleonora's Falcon (F. eleanorae), a plate of such would have been valuable.

My opinions of David Digby's artwork are similar to those of the text: the paintings range from mediocre to exceptional. This range can be seen within a single painting: Plate ii shows a fine adult Prairie Falcon (F. mexicanus) feeding three rather odd looking young (note the inconsistency of bill morphology). The colors of several paintings are too rich (e.g., the Merlin [F. columbarius], Plate XV). Otherwise, most of the paintings are excellent, worthy of a text by Cade. In many cases Digby superbly captures certain postures which are truly typical of falcons.

In summary, The Falcons of the World is of exceptionally high quality, combining some of the finest in writing and art in a book of this kind. My criticisms aside, considering the magnitude of the task, this is a remarkable effort.—GARY R. BORTOLOTTI.
Woodpeckers of the World. By Lester L. Short, illus. by G. Sandström. Delaware Museum of Natural History Monograph Series Number 4, Greenville, Delaware, 1982: 676 pp., 101 color plates, 2 tables. $99.95 (order from Foris Publications USA, Box C-50, Cinnaminson, New Jersey 08077).—Few taxa of birds have a more devoted follower than Lester Short, who has been pursuing members of the family Picidae throughout most of his 30-year professional career and around a great deal of the world (with the exception of Australia and Antarctica, both suffering from an inherent deficiency in woodpeckers). This book, the culmination of these indefatigable efforts, is a semitechnical “handbook,” summarizing both Short’s own extensive work and other pertinent literature on the family. There are three main sections to the book; the first, 56 pages long, is an introduction to the biology of woodpeckers, briefly covering plumage, structure, behavior, zoogeography, evolution, and systematics. I found this section a curiously mixed bag: 2 pages on terminology discuss “feathers,” “behavior,” and “size,” but send the reader to an ornithology textbook to review most of the external parts of a bird despite the subsequent detailed technical diagnosis of the family as well as of each individual species. The social mimicry/character convergence models of Moyrihan (Evolution 22: 315–331, 1968) and Cody (Condor 71: 222–239, 1969) are cited as the likely explanation for the extensive plumage similarities observed in woodpeckers (p. 9), despite the controversiality of these hypotheses and the fact that Short himself later appears to abandon them (p. 33). The behavior section focuses on displays, vocalizations, and other aspects of classical ethology and references the author’s own work extensively and nearly to the exclusion of others (16 of 22 references in this section are to Short’s papers). Sociality in the family is suggested to be variously related to frugivory and omnivory (p. 23) and to habitation of an “. . . open, essentially uniform environment” (p. 19) with no citations or attempt to test these hypotheses. Interspecific aggression over nests ceases when both individuals have secured holes because “. . . it is inefficient for both species to continue interacting aggressively” (p. 32). Although the section on zoogeography, evolution, and systematics is detailed and authoritative, being once again primarily a review of Short’s work in this area, it avoids all but a superficial discussion of the fossil record or of evolutionary origins of woodpeckers. Short defends his reliance on external morphology and behavior as taxonomic characters by suggesting that biochemical techniques, among others, are at a stage precluding robust evolutionary interpretations—a stance I would not like to be caught professing in the current golden age of electrophoretic and DNA-DNA hybridization studies.

Perhaps the biggest disappointment afforded by this section of the book is Short’s reluctance to summarize in quantitative terms the massive amount of data collected in the species accounts that follow. Two tables, one summarizing the geographic distribution of the genera of woodpeckers by faunal region and the other listing the number of species by size class in each faunal region, are as far as he goes towards synthesizing the vast store of information he opens up in the succeeding section. For example, statements that there is a “reduction, or even elimination of a pattern [of sexual dichromatism], in highly social species” (p. 12) and that “differences between the sexes are especially pronounced when few or no other woodpeckers occur sympatrically” (p. 14) are intriguing, and sometimes considered to be common knowledge, but in any case beg to be tested by going through the species accounts that follow and compiling the necessary data. Without such documentation these statements are not always convincing. However, Short’s hesitancy provides an open opportunity for others, and I, for one, will not be able to resist using the book this way for long.

The bulk of the book (480 pp.) consists of accounts of all 198 species in the family, or slightly under 2.5 pages per species. For each species, there is a list of diagnostic features, a detailed description, a summary of its distribution and habitat, and sections on foraging habits, voice, displays, interspecific interactions, breeding, and taxonomy. This section is clearly the real meat of the book, and a considerable amount of information is buried within
these accounts. However, such basic information as size and weight is lacking or at best given as ranges only, forcing one to return to Ridgway and others for information on mean size and precise degree of sexual dimorphism. Other material is at times difficult to follow. For example, no range maps serve to help the reader visualize geographic distributions; instead, lists of localities often seem to stretch on interminably. Older yet, the species descriptions are often tantamount to technical diagnoses worthy of type specimens. A typical account begins: "Bill moderately long, slightly curved along culmen, small chisel-tip, and broad across nostrils. Black band across uppermost back, then black and white barred posteriorly to rump; lower rump and uppertail coverts black. Wings black with white spots or spot-bars on coverts, white bars elsewhere; paler below, gray with white bars . . . " etc. These descriptions, although valuable when distinguishing among subspecies or similar-plumaged forms, are generally enough to send anyone packing to the color plates without delay. I had a similarly difficult time maintaining my concentration throughout the "voice" and "display" sections of each species account. No sonograms are provided to pull together the myriads of "wickers," "twitter," "rattles," "wads," "whew-whews," "wuk's," and other vocalizations discussed in extensive detail, often including call duration, frequency, rate of delivery, and a verbal description. The "breeding" sections are generally more diverse and interesting, suffering primarily from a lack of information on many of the species—truly a challenge to picidologists of the future—and a dated quality discussed below.

Unsurprisingly, the most consistently solid parts are those on taxonomy, where Short details his views on the relationships and closest relatives of each taxon. It is certainly useful to have all of Short's extensive knowledge and work on the taxonomy of these birds summarized in one place, although once again range maps would have been helpful in order to visualize how closely related forms mesh with one another.

In my view, the most serious shortcoming of the book is its datedness. Short has thoroughly researched the literature, including some obscure European and Southeast Asian journals rarely seen by western ornithologists. Unfortunately, the bulk of Short's review apparently ended somewhere in the mid-1970s. There are only 13 references dating from 1976 on, five of which are to Short's own papers; otherwise, of 387 references to work other than Short's, 76% date prior to 1970. In some cases this results in quaint anachronisms in the species accounts; for example, referring to the displays of the Acorn Woodpecker (Melanerpes formicivorus), he states that "very little detailed information is available; known displays seem very similar to those I have described . . . for M. cruentatus." This section was obviously written prior to the treatise of MacRoberts and MacRoberts (Ornith. Monogr. 21, 1976), much less subsequent work on this species, and never updated. Partially as a result, there is scant attention devoted by Short to any of the more recent behavioral ecology being done on various species of woodpeckers and only references to some of the older literature on foraging ecology.

Finally, 101 color plates fill the end of the book. Although not all of the paintings capture my vision of the "soul" of woodpeckers, and none include backgrounds other than a limb or trunk for the birds to sit on (probably because disjunct but related forms are often put together), they are in general a tour-de-force of biological and artistic illustration. Each includes two to five related forms or plumages of the same form, allowing easy comparison among closely related taxa.

In summary, the usefulness of this book to the majority of professionals is limited by its datedness and lack of summaries of morphological or behavioral data. Furthermore, despite the rather steep price, the book does not rank aesthetically among the most elegant monographic treatises of the past decade; the format and style are simply not of a sort to make it a prized "coffee-table" book.
However, I can fully recommend this monograph as a valuable reference for woodpecker aficionados, and I personally am looking forward to tapping the information contained in it in the future. Certainly anyone interested in surveying the biology of these birds should have access to a copy, as it will no doubt be the standard reference on the family for many years to come.—WALTER D. KOENIG.

A CELEBRATION OF BIRDS. By Robert McCracken Peck. Walker and Co., New York, New York. 1982: 178 pp. $30.00 cloth.—The subtitle tells what this book is all about: The life and art of Louis Agassiz Fuertes (1874–1927), who is regarded by many as America’s premier nature artist. It was written to accompany a collection of Fuertes originals exhibited by the Academy of Natural Sciences of Philadelphia. After a home showing in the autumn of 1982, the exhibition has been taken on the road and will provide pleasure in six cities before returning home in February 1985.

The exhibit and book present representative and often heretofore unexhibited Fuertes paintings from collections throughout the country. In addition to the works of art, photographs, letters, and journal materials are included. The color registry is very good. Like many books today, the printing was, regrettably, done in Hong Kong. The half-title page has a reproduction of Fuertes’ bookplate—a nice touch. The frontispiece is a watercolor study of the Red-breasted Merganser. The acknowledgments are followed by a table of contents which indicates that the text will treat Fuertes as the Man, the Artist, and the Naturalist. The foreword by the President of the Academy, Thomas P. Bennett, explains the structuring of the Fuertes exhibit and how this book relates to it. Roger T. Peterson provides the introduction with erudite comparisons among several of this country’s outstanding bird artists. Peterson confides, “It was largely because of the Fuertes portraits that birds became the focus of my life . . . .” This is another debt today’s bird students owe to Fuertes.

Peck guides the narrative with an historian’s skill, enlightening without intruding into the events that allow the reader to know Fuertes as a man, an artist, and a naturalist. This threepart format at first appears to be a logical and interesting approach to a biography, but even Peck’s easy prose cannot avoid redundancy, and one must approach each part as a separate account rather than a continuous epic.

Perhaps Fuertes’ most outstanding personal aspect is that he was self-taught. He was doubtless aided in his art by an association with the artist Abbott Thayer, but in the final analysis he was his own man. I would like to have learned more about his growth as an artist and particularly why he eventually (p. 38) was rejected by Thayer—was it personal or professional? Whether Fuertes could have been the classical artist that Thayer hoped he might be is of course moot, but I feel as did Gilbert Grosvenor that “. . . Fuertes could accomplish anything he put his mind to.”

To be championed by such stalwarts in ornithology as Coues, Chapman, and Merriam gave Fuertes intellectual, moral, and on occasion, financial support. No other bird artist had such assists at any time in ornithological history.

In examining the art work presented it is necessary to distinguish among sketches, colored studies, and completed paintings. Perhaps one of the finest paintings shown adorns the cover of the dust jacket. To study this painting of a white Gyrfalcon (Falco rusticolus) in minute detail is to be taught a lesson in bird painting. The feather detail, feather arrangement into units, color of the tail in shadow, the raptor personality in the head, the crumpled talon of the supporting foot and the eye highlighting are the artistic insights of a master. It is not a
portrait alone; the color, composition, and setting make it an exciting painting. The same Gyrfalcon reproduced on p. 26 is washed out by comparison with this bird that dominates the dust jacket.

The male Harlequin or Mearn's (= Montezuma) Quail (Cyrtonyx montezumae) appears three times in the book (pp. VIII, 57, 106), twice in color. Having worked with this species in the wild in Mexico and in an aviary in the U.S., including the preparation of museum skins, I rate all three below average for Fuertes. The painting opposite the foreword is the best, but the spotting is unlike any that I ever saw and the bird lacks lifelike qualities Fuertes gave to his birds. On p. 57 the overall color is more gray-green than I remembered and the background and brown color in the watercolor study are more typical than in the final painting. The black and white plate of a colored painting (p. 106) has the bird at 3/4 face giving it a peculiar and distracting appearance.

The painting of the Roadrunner (Geococcyx californianus) in full stride with both feet in the air gives one the impression that he has just seen the bird captured by strobe flash. Although the picture is almost a cartoon, nothing is exaggerated and no anatomy violated.

A very handsome painting of a Peregrine Falcon (F. peregrinus) with a captured Green-winged Teal (Anas crecca) (p. 97) is a hit puzzling. The falcon is immaculate, but the teal should have a wide green patch that runs from an area in front of and including the eye backward and downward ending in a slight crest below the base of the skull. The teal in the painting has a white patch that does not start in the front of the eye and the exposed wing, with more white feathers than a teal possesses, appears to be that of an American Wigeon (A. americana). Could this have been an unfinished painting, where green paint was not overlaid? Or, possibly the green pigment has faded. It is virtually inconceivable to me that Fuertes would mispaint a Green-winged Teal.

There are many subtleties in the art of bird painting to be found in the work of Fuertes. In his preliminary sketches of the Common Potoo (Nyctibius griseus) (p. 127) the bird is drawn several times in profile but in the final painting (p. 128) the viewer looks up at the bird perched on the end of an upright snag. Here the viewer sees the large eye as though it were the setting sun with the lower portion below the horizon of the lower eyelid.

Fuertes' bird portraits reproduced on small cards and found in boxes of Arm and Hammer baking soda in the 1920's were teaching collectibles that predated "baseball cards." I suspect that their impact on audiences of all ages and backgrounds rivaled that of field guides to birds by other artists in years after his death. Fuertes' first and best known protege was the gentle George Miksch Sutton, who incorporated the skills learned at Fuertes' elbow into his own outstanding artistry. Peck treats this association between teacher and pupil with a sensitive understanding.

One of the threads in the fabric of Fuertes' life as presented are the letters in his hand or those written to him. Peck's ability to select the salient features of Fuertes' correspondence in order to focus on the artist as a person is a major strength of the book.

Expeditions and field trips found Fuertes in his element. One of these was the Harriman Alaskan Expedition of 1899. A member of that expedition, Leon J. Cole, listed as a preparator in the crew, was a personal friend of mine and told this story. The working group (e.g., naturalists, artists, preparators, etc.) had forgotten to take a deck of cards aboard, so one evening when a game was called for, Fuertes got out his paints and brushes and produced a deck from a pad of paper. They were beautiful and relatively little used when they were shown to me by Leon Cole about 1945.

At the end of the text Peck provides a chronology of Fuertes' life: what institutions have collections of his paintings; a list of illustrations from the book and the owners of the original work; a series of notes that are referenced in the text; a selected bibliography; and finally a
detailed three-page index. This book and its contents reaffirmed a long-held personal opinion that Louis Agassiz Fuertes was the best bird artist ever.

You would reward yourself and honor your bookshelf with this story of the life and art of Louis Agassiz Fuertes.—ROBERT A. McCABE.

AVIAN INCUBATION: EGG TEMPERATURE, NEST HUMIDITY, AND BEHAVIORAL THERMOREGULATION IN A HOT ENVIRONMENT. By Gilbert S. Grant. Ornithological Monographs No. 30. The American Ornithologists' Union, Washington, D.C., 1982:x + 75 pp., 15 tables, 35 figures. $9.00 ($7.00 to AOU members).—The Salton Sea in southern California is a man-made, saline lake surrounded by Sonoran Desert. Because of low humidity and infrequent cloud cover during the summer, solar radiation is intense. Temperature of the ground near the Sea regularly reaches 50°C, and air temperature commonly exceeds 38°C. Despite the apparent harshness of this environment, however, several species of ground-nesting birds successfully produce young here.

Gilbert Grant has undertaken a comprehensive study of the common species of birds nesting on the shores of the Salton Sea: (1) to determine whether eggs, young, or adults experience thermal stress; (2) to assess the effects of different environmental variables on temperature of eggs and adults; and (3) to evaluate the physiological and/or behavioral mechanisms that minimize negative impacts of the hostile thermal environment. His success in achieving these several goals was mixed.

The detailed analysis of behavior of adult birds is the strength of the study, and illustrates the power of careful observation. Grant develops an especially strong case that adults of several charadriiforms prevent incubating eggs from over-heating by transporting water to nests in their abdominal feathers. The water is applied to surfaces of eggs, and air flowing over these surfaces causes evaporation, thereby dissipating excess heat. The attending parent remains crouched above the eggs to shade them from the sun and other environmental radiation, because exposure of eggs for as little as 2 min can lead to explosive rise in temperature and death of embryos.

Laboratory phases of the investigation are weaker, despite their importance to the overall study. In part, this situation exists because of the distance of the study site from adequate facilities. In part, however, it reflects flaws in experimental design and/or analysis. For example, samples are too small in several of the experiments to provide compelling support for any conclusion whatsoever (e.g., effects of salt and mud applied to surfaces of eggshells on oxygen consumption of embryos), and some differences among means are reported to be significant without any mention of the statistical procedure on which the claim is based (e.g., daily loss of mass and water-vapor conductance). Some of the regression equations reported in Figs. 9–10 clearly are statistically spurious, indicating that the author relied more on levels of significance in assessing the outcome of his analyses than on inspection of the data or on values for coefficients of determination. Many of the data for water-vapor conductance and other physical properties of eggs are compared with expectations based on published allometric equations; unfortunately, by pooling data for clutchesmates, Grant introduces important biases into his analyses that preclude meaningful comparison with prior work (see Sotherland et al., Auk 96:192–195, 1979).

In summary, Grant's investigation is one of the most ambitious undertakings of its type, and it provides important perspective for those of us interested in problems of development in nature. However, not all of his conclusions are adequately supported by evidence, so readers must examine the data thoroughly and critically.—GARY C. PACKARD.
BIRD HABITATS IN BRITAIN. By R. J. Fuller, illus. by Donald Watson. T. & A. D. Poyser, Calton, Staffordshire, England (dist. in U.S.A. by Buteo Books, Vermillion, South Dakota 57069), 1982:320 pp., 56 black-and-white drawings, 79 text figures. 55 tables. $35.00.—The data for this work were collected by the impressive efforts of the British amateur ornithology "machine," co-ordinated by the British Trust for Ornithology (BTO), its research advisors, the author in his capacity as national organizer, and the 104 regional organizers. This network of observers has been built up over many years of BTO enquiries, its efforts culminating in "The Atlas of Breeding Birds in Britain and Ireland" (J. T. R. Sharrock, T. & A. D. Poyser, Calton, Staffordshire, England, 1976). One goal of the "habitat register," which provided data for the book under review, was to expand on the species presence/absence records of the atlas by full yearly coverage of many selected sites throughout Britain, thus providing at least an index of bird species abundance in each season. The second, and perhaps the most important goal, was to provide data on the majority of significant ornithological sites in the country. These data were deposited with the British Nature Conservancy (i.e., government) to be included at the initial planning stages in any review of proposals for major habitat alterations. The relative ornithological importance of the ca. 4000 sites covered from 1973–1977 was also assessed by Fuller and included with the bird and habitat data.

Fortunately, the book is not an endless compilation of species lists from all the sites; these are where they belong, in a computer. The first 13 chapters summarize the bird communities of major habitats, e.g., neutral grasslands, rocky coastlands, lowland heaths, lakes, etc. Greatly altered habitats such as farmland and urban areas are not included, although the point is well made that there is very little of Britain that has not been altered by man in some way. We learn, for example, that the destruction of woodland started with the advent of Neolithic cultivation in 3000 B.C. Commonly occurring bird species are discussed under the headings of breeding, wintering, and passage. The major species assemblages are often presented graphically with frequency of occurrence plotted against the index of abundance for each species. Subdivisions of each habitat are made when appropriate. Other summary figures used (when sample sizes allow) include: breeding birds vs tidal zones, breeding density vs tree species, species diversity vs foliage height diversity, incidence of breeding species vs woodland area, breeding bird density vs successional stage of sessile oakwood, distribution of concentrations of seaduck around the coast, plus many other such correlations. Information gathered by the habitat register is supplemented in the book by results from such other BTO studies as the Common Bird Census, Nest Record Cards, Atlas, and Bird Ringing.

Chapter 14 summarizes the structure and composition of bird communities throughout the country. Chapter 15 is an evaluation of bird sites and chapter 16 shows their distribution in England, Wales, Scotland, and the Isle of Man. It is regrettable that the book could not cover Ireland, as did the Atlas. Appendices include the methods of site recording, methods of analysis and the samples of sites used in the text: plus 55 tables for those who wish to inspect the preliminary data.

Taken overall, the text is interesting and readable. the conclusions follow the data presented, the references are copious and pleasingly international. The statement on p. 62 that "trees themselves are the dominant feature of the woodland ecosystems," struck this reviewer as a fairly obvious point, but this was an isolated example within a non-technical but accurate text. Figures were prepared clearly by Murray and Baker, the latter preparator also enlivened many figures with very pleasing vignettes, while Donald Watson's illustrations bring to life both the birds and the habitats described. R. J. Fuller and the BTO have presented ornithologists in all countries with another challenge and a new direction in field ornithology.—TREVOR L. LLOYD-EVANS.
THE BIRDS OF DORSET. By Col. E. D. V. Prendergast and J. V. Boys. David & Charles Inc., North Pomfret, Vermont, 1983:256 pp., $32.00.—Dorset is a nearly Rhode Island-sized, largely agricultural county along the south coast of England. Its rich ornithological history dates to St. Aldhelm (d. 709), who wrote about four species occurring there of the 16 which had been named by that time. The most recent comprehensive accounting of the birds of the area prior to this work was published in 1888, and the authors’ objective is to reflect changes in the environment and the avifauna since that time.

In addition to an annotated list of the more than 360 species confirmed for the county through 1978, “The Birds of Dorset” contains essays on eight of its regions, each written with a different focus by a different guest author. There is also a chapter on migration in Dorset based in part on the work of the Portland Bird Observatory, established in 1955 on a narrow peninsula extending several miles into the English Channel. A discussion of the prospects for the future of Dorset’s environment concludes rather optimistically that society is both able and willing to function while respecting both the landscape and its wildlife.

Although the writing in this book is uneven and the treatment of some of the topics is superficial, “The Birds of Dorset” is a useful reference point in the ornithohistory of the area. Anyone interested in local distribution of birds within Britain, or having personal ties to Dorset, may want a copy despite its price.—P. WILLIAM SMITH.

MARINE BIRDS AND MAMMALS OF PUGET SOUND. By Tony Angell and Kenneth C. Balcomb, III. Washington Sea Grant, Seattle, Washington 1982:xiii + 146 pp., black-and-white illustrations, range and habitat maps, 7 tables, bibliography, index, paperback. $14.50 (available from University of Washington Press, Seattle, Washington).—At first glance, this book appears to be of only local interest. Upon closer examination, the reader realizes that this story of marine birds and mammals at Puget Sound is common to many localities. The authors not only describe the marine mammals and birds of the area, but place them in an environment that is becoming more polluted and changed by human progress.

The description of Puget Sound begins with the historical role of the local fauna in the mythology and lifestyle of the West Coast Indians, and then brings us to the present perils faced by the wildlife as a result of human infringement on habitats. Complete descriptions and locations of various natural habitats and communities are given along with the types of pollution, their sources, and the existing and potential effects on the marine life in general.

Twenty-three families and sub-families of marine birds and seven families of mammals are described. Each family is summarized in general terms; then species found in the Puget Sound area are covered in greater detail with a few paragraphs outlining their status, distribution, diet, and critical habitat. Local distribution maps are included in the marine bird section.

The descriptions of the birds include the critical factors that could disrupt their habitats or feeding routines (oil spills, dissolved chemical pollutants, etc.). This section also includes many personal anecdotes and very descriptive language that almost bring the birds soaring out of the pages. The mammals section, on the other hand, is much more precise and objective, though no less effective. The sections reflect the different backgrounds of the authors. One is a writer and artist with an interest in natural history, and the author of various articles and books on birds. The other is a zoologist who has concentrated his studies on whales and other marine mammals. The difference in style almost makes this two books within one cover. If this is what the authors were striving for, they achieved it. If not, proper editing was lacking. The illustrations by Tony Angell do maintain a continuity throughout the book and are an attractive addition.
The last section of the book includes tables summarizing the life histories of the marine mammals and the impacts of pollution, humans, and habitat loss. The types of preferred habitat, feeding strategies, breeding seasons, and periods of greatest abundance for all the mammals and birds covered in the text are also summarized in tabular form. This summary along with the maps of the main marine vegetation and wildlife areas will provide a local nature enthusiast with enough information to go looking in the right places for wildlife. Enthusiasts would be advised to take bird and mammal field guides with them though, since the book, measuring $28 \times 21.5$ cm, is not designed for hikers or boaters. The descriptions of the fauna are not suited for quick field identification.

This is the third of a 14-volume series about Puget Sound aimed at educating the public about the area. In this context, the authors are very successful at bringing the marine wildlife and their delicate existence to the public eye. It is not too technical and would be a good reference book in a school or public library, and in local industrialists’ offices. For those with a deeper interest, the bibliography provides an adequate list of books and papers as a starting point for further reading.—ALLAN WERDEN.

**Finding Birds in the National Capital Area.** By Claudia Wilds. Smithsonian Institution Press, Washington, D.C., 1983:215 pp., numerous black-and-white drawings and maps, paper covers. $10.95.—This is a guide to finding birds in the vicinity of Washington, D.C., including not only the city, but adjacent areas of Maryland, Delaware, and Virginia. After a brief introduction to the region, including geography and climate, the bulk of the book is devoted to chapters detailing birding areas, with maps and specific instructions for finding different sites, and comments on the kinds of birds to be expected there. There are also chapters on special pursuits, including pelagic trips, sites for watching hawk migration, and owlving. Appendixes list natural history and ornithological societies, useful publications, and cooperative birding activities. This nicely printed book should prove a useful reference for birders in the District of Columbia and adjacent regions.—R.J.R.

**Birds of Central Pennsylvania,** Third Edition. By Merrill Wood. Records of the State College Bird Club, Inc., 1983:82 pp., 2 maps, paper covers. Price not given.—This is an updated compilation of bird records for the area within a radius of 40 km (25 mi) of Old Main on the campus of The Pennsylvania State University. Species are listed according to the 6th edition of the A.O.U. checklist, but are given by common name only. Information includes status, abundance, seasonal occurrence, and habitat. For mail orders direct inquiries to Dr. David L. Pearson, The Pennsylvania State University, 312 Mueller Laboratory, University Park, Pennsylvania 16802.—R.J.R.

**New Journal.—Ontario Birds.** Publ. by Ontario Field Naturalists, P.O. Box 1204, Station B, Burlington, Ontario L7P 3S9, Canada.—This attractively printed new journal is meant to stimulate bird study in the province. It is especially intended to provide information on “the status of bird species in Ontario, significant provincial or county distributional records, tips on bird identification, behavioural observations of birds in Ontario, location guides to significant birdwatching areas in Ontario, book reviews and similar material of interest on Ontario birds.” It is sent to all members of the Ontario Field Naturalists. Direct inquiries to the address given above.—R.J.R.
ENCyclopedia of Aviculture. By Richard Mark Martin. Arco Publishing, Inc., New York, New York, 1983:228 pp., 93 text figures. $14.95.—In this surprisingly small volume Richard Mark Martin has presented a wealth of information on aviculture. If he hasn't touched upon almost every species that has been kept, as well as all other aspects of the subject, he has certainly come close to it.

Entries are arranged alphabetically, and are conveniently cross-referenced. If one looks up aspergillosis, he is referred to the more general topic of respiratory disorders. The entry Carduelinae, on the other hand, directs one to Fringillidae, Bullfinch, canary, goldfinches, grosbeak, Linnet, Rosefinch, Serin, Singing-Finch, siskin, crossbill, and Trumpeter Finch. Scientific names, as well as common names along with frequently encountered synonyms are given. Throughout the text, topics or species that are used as headings elsewhere are capitalized.

Martin strictly limits his discussions to aviculture, providing only minimal comments on natural history and distribution. Each species, or broader group, is covered in terms of systematic position, dietary requirements, appropriate accommodations, breeding behavior, and any other points that would be helpful to a prospective keeper. Broader topics, such as over-crowding, endoparasites, or viral diseases, are discussed in the context of aviculture.

Martin has been successful in aiming his book at both amateur and professional aviculturists. It is relatively free of technical zoological vernacular, but quite impressive in the accurate, up-to-date presentation of breeding records, newly discovered subspecies, and avian classification.

The book does have one very unfortunate deficiency. The bibliography is extremely limited and references within the text are infrequent. Since Martin provides only a brief account after each entry, references to more detailed works, beyond the scope of his book, would have been appropriate. Brevity would not have been sacrificed, while the information presented would have increased several-fold, making the book a true gem.

I recommend this book for anyone interested in aviculture at any level, and for both neighborhood and academic libraries. At $14.95 it's a bargain.—Susan L. Berman.

PROCEEDINGS OF THE SIXTY-FOURTH ANNUAL MEETING

CURTIS S. ADKISSON, SECRETARY

The Sixty-fourth Annual Meeting of The Wilson Ornithological Society was held Thursday, 2 June to Sunday, 5 June 1983, at the University of Wisconsin—Green Bay, in Green Bay, Wisconsin. The University hosted the meeting, and the Local Arrangements Committee consisted of Theresa Duffey, Tom Erdman, Kathy Stiehl, and Richard Stiehl, Chairman.

The meeting opened on Thursday evening with a cheese and wine reception, featuring some famous Wisconsin cheese varieties, in the Nicolet Room of the University Commons. On Friday, following early morning field trips, the first business meeting was held. The Society was welcomed by Dr. Edward W. Weidner, Chancellor of the University of Wisconsin—Green Bay. President Abbot S. Gaunt responded for the Society. After the first business meeting, the paper sessions began.

During the meeting there were several special events. Friday evening there was an informal fish boil, a culinary specialty of northeastern Wisconsin. Films on ornithological and con-
servation topics were shown later that evening. The Richter Natural History Collection was open for tours Thursday and Saturday. The spouses' program featured a tour of arts and crafts shops on the Door Peninsula on Friday morning, and trips to Heritage Hill State Park and to the Neville Public Museum on Saturday.

There were early morning field trips around campus, and on Sunday, trips to the Door Peninsula's boreal habitats and to marsh habitats on the western shore of Green Bay.

The annual banquet was held Saturday night, in the Nicolet Room of the University Commons, after which there was a slide presentation by Mike Putnam on the work of the International Crane Foundation, especially on the rearing of a young crane.

At the banquet, President Gaunt announced the following awards:


Two equal awards were made, and these went to:


LOUIS AGASSIZ FUERTES AWARDS

Janice R. Crook, SUNY, Syracuse, "Helping and infanticide in the Barn Swallow (Hirundo rustica)."

Patricia McGill-Harelstad, Cornell University, "Breeding ecology and interspecific interactions of three Australian gulls: parallels with a northern system."

STEWART AWARDS

Jeffrey Martin Black, The Wildfowl Trust, Slimbridge, United Kingdom, "Autumn migration mortality in Barnacle Geese with special reference to family behavior."

Opal H. Dakin, Mississippi State University, "Nesting phenology, nest-site selection, and reproductive success of starlings in Mississippi."

Kathryn A. Daniels, Bowling Green State University, "Components of reproductive effort: effects of clutch-size and brood-size on survival of adult House Wrens (Troglodytes aedon)."

James B. Devereux, Whitefish Point Bird Observatory, Paradise, Michigan, "Spring raptor migration at Whitefish Point, Michigan."

Timothy Carl Lamey, University of Minnesota–Duluth, "The effects of Great Horned Owl (Bubo virginianus) predation on the behavior of colonial nesting gulls and terns."

Bette A. Loiselle, University of Wisconsin–Madison, "Seasonal variation in composition of bird communities along an elevational gradient in a Costa Rican rain forest."

Christopher C. Rimmer, University of Minnesota–Minneapolis, "Prebasic molt strategies in a boreal passerine community."

ALEXANDER WILSON PRIZE (for best student paper at the meeting)

Two papers were judged deserving of this prize:

Richard L. Knight, University of Wisconsin–Madison, "Responses of nesting ravens to different levels of human activity."

Susan K. Knight, University of Wisconsin–Madison, "Daily activities of White-tailed Ptarmigan during the breeding season."
FIRST BUSINESS MEETING

The first business meeting was held on 3 June 1983, President Abbot S. Gaunt presiding. He announced the posting of a list of proposed new members, and the appointment of the Alexander Wilson Prize and Auditing committees. He also urged those interested in formulating resolutions to contact Nancy Mueller of the Resolutions Committee.

Secretary Curtis S. Adkisson then summarized actions of the Council: Jon C. Barlow was re-elected Editor of The Wilson Bulletin. Council voted to establish an annual competition in ornithological art in memory of the late George M. Sutton, past president of the Society. The competition will consist of paintings and drawings to be shown at the Society's annual meetings, to be judged by a committee of experts. The winner of the Sutton Award will receive a cash prize of $500.00.

Robert D. Burns then presented the Treasurer's report.

REPORT OF THE TREASURER
1 JANUARY 1982 TO 31 DECEMBER 1982

GENERAL FUNDS

RECEIPTS

Dues collected in 1982
Student and Regular Membership for 1982 .......... $ 11,043.50
For 1983 .................................. 12,783.50
Family Membership for 1982 ..................... 160.00
For 1983 .................................. 300.00
Sustaining Membership for 1982 ................. 1,846.00
For 1983 .................................. 948.00
TOTAL DUES ................................ $ 27,081.00
Subscriptions to The Wilson Bulletin
For 1982 .................................. $ 5,273.50
For 1983 .................................. 4,881.50
TOTAL SUBSCRIPTIONS ......................... $ 10,155.00
Back issues of The Wilson Bulletin .............. $ 2,317.59
Interest and Dividends ........................ $ 22,888.64
Royalties .................................. $ 251.29
Contributions from Authors ..................... $ 1,023.86
Contributions to the Student Awards Funds ...... $ 2,440.00
Contributions to Endowment and Life Memberships $ 3,227.00
TOTAL RECEIPTS—1 Jan.–31 Dec. 1982 .......... $ 69,384.38

DISBURSEMENTS

The Wilson Bulletin
December 1981 .................................. $ 11,041.03
March 1982 .................................. 8,372.09
June 1982 .................................. 9,540.23
September 1982 ............................... 13,092.80
Colorplates .................................. 3,316.56
Insurance .................................. 23.00
Return Mailing and P.O. Permit ................. 33.50
Editorial Assistants .......................... 1,200.00
TOTAL PRODUCTION COSTS .................. $ 46,619.21
### Annual Report

#### Additions to Endowment Trust at Central Counties Bank
- $3,227.00

#### Deposit of Student Awards Funds to Dreyfus Liquid Assets
- $2,440.00

#### Deposit to Awards Funds from Endowment Earnings
- $3,250.00

#### 1982 Incorporation Fee
- $5.00

#### Dues to International Council for Bird Preservation 1982
- $100.00

#### Editor’s Expenses
- Telephone: $246.86
- Travel: $354.46

#### Treasurer’s Expenses
- Postage and Secretarial Service: $502.61
- Student Membership Mailing: $40.00
- Ornithological Societies of North America: $9,628.22
- Treasurer’s Bond: $37.00

#### Total Disbursements—1 Jan.–31 Dec. 1982
- $66,450.36

#### 1982 Income Surplus
- $2,934.02

### Cash Accounts

**Checking Account, 31 December 1982**: $147.27

**Savings Account, 31 December 1982**: $9,363.29

**Dreyfus Liquid Assets, 31 December 1982**: $49,721.17

**Total Cash on Hand**: $59,231.73

### Designated Accounts

#### Van Tyne Memorial Library Fund

**Receipts**
- Balance 1981: $564.45
- Sales and Gifts: $736.30

**Disbursements**
- Purchase of Books: $682.12

**Balance**: $618.63

#### Louis Agassiz Fuertes Research Fund

**Receipts**
- Endowment Earnings: $400.00

**Disbursements**
- Stephen Nowicki: $200.00
- Brian McCaffery: $200.00

#### Margaret Morse Nice Fund

**Receipts**
- Endowment Earnings: $200.00

**Disbursements**
- Michael Facemire: $100.00
- A. Townsen Peterson: $100.00

#### Alexander Wilson Prize

**Receipts**
- Endowment Earnings: $100.00
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**Aaron Bagg Student Award Fund**

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SECOND BUSINESS MEETING

The second business meeting was called to order by President Gaunt on Saturday afternoon, 5 June 1983. The proposed new members of the Society were elected unanimously. Four resolutions presented by the Resolutions Committee were approved unanimously. The report of the Auditing Committee was also approved unanimously. These reports and summaries of other committee reports to Council are presented below.

The second business meeting ended with the report of the Nominating Committee, chaired by George A. Hall. He presented the slate of officers for 1983–84: President, Jerome A. Jackson; First Vice-President, Clait E. Braun; Second Vice-President, Mary H. Clench; Secretary, Curtis S. Adkisson; Treasurer, Robert D. Burns; Elected Member of Council (term to expire in 1986), Mitchell A. Byrd. There were no further nominations, and it was moved, seconded, and passed that the Secretary be instructed to cast a unanimous ballot for the slate.

AUDITING COMMITTEE REPORT—1982

We, the undersigned, have reviewed and validated the balances of The Wilson Ornithological Society, submitted by the Treasurer for the calendar year ending 31 December 1982. We are satisfied that these accounts accurately represent the financial transactions and assets of the Society.

The Auditing Committee wishes to commend the Treasurer, Dr. Robert D. Burns, for successfully fulfilling his responsibilities as Treasurer.

William A. Klamm, Member
Hubert P. Zernikow, Member
Harold Ratcliff, Member
Robert A. Whiting, Member

EDITOR’S REPORT—1982

In 1982 The Wilson Bulletin contained 650 pages, including 32 major papers, 61 notes, 31 reviews, an index, and an account of the holdings of The Josselyn Van Tyne Memorial Library at the University of Michigan, Museum of Zoology. During the year 160 manuscripts were received. The enormous task of processing these manuscripts was accomplished with the cooperation of an editorial staff consisting of: Margaret May, Nancy Flood, Gary Bortolotti, Keith Bildstein, Richard Snell, Janet Mannone, Dave Ankney, Jim Rising, and Peter Fetterolf. Robert Raikow and William Lunk continued as Review Editor and Color Plate Editor, respectively. I am grateful to these people, and to all those who reviewed manuscripts for the Bulletin during the year, as well as to the Royal Ontario Museum for cooperation in many ways.

Editing The Wilson Bulletin is a rewarding, albeit time-consuming activity. Due to the press of additional responsibilities, I must submit my resignation as Editor with the completion of Volume 96 (1984). Thus, the Society needs to find a new Editor able to receive manuscripts in April, 1984.

Jon C. Barlow, Editor

LIBRARY COMMITTEE REPORT—1982

The activities of the Josselyn Van Tyne Memorial Library went as smoothly as usual, thanks largely to the constant care and dedication of Janet Hinshaw, who, in addition to her

Once again, we thank the membership for its fine support, but urge more use of our ever-growing facilities and, if possible, broader member support for them.

William A. Lunk, Chairman

MEMBERSHIP COMMITTEE REPORT—1982

Total paid membership for the Society was 2231 in the calendar year 1982, including 218 new members. I handled 36 requests for membership applications since our last meeting. Applicants were sent our membership prospectus detailing the activities of the Society and describing the classes of membership, and a letter asking them to send dues to OSNA in Ithaca, New York. The Committee designed a new membership brochure and poster display, both available at the annual meeting. I encourage anyone interested in using our new display at local meetings to write to me.

Keith L. Bildstein, Chairman

STUDENT MEMBERSHIP COMMITTEE REPORT—1982

Announcement of the availability of the Aaron M. Bagg Student Membership Awards was made in The Wilson Bulletin and the Ornithological Newsletter. In addition, information about the award and application blanks were sent to 171 members of the Wilson Society situated in positions affording identification of nominees for this award. Application materials were also sent in response to inquiries from prospective applicants. There were 39 eligible applicants, with candidate materials being evaluated independently by the four members of the committee. There were funds available for 14 awards. The following received Aaron M. Bagg Student Membership Awards in this year’s competition: Steven R. Beissinger, Univ. Michigan; Theodore Thomas Buerger, Auburn Univ.; Ann Marie Francis, Univ. Wisconsin; R. Given Harper, Western Illinois Univ.; Bradley G. Hill, Univ. Calgary; Lee Richard Jones, Utah State Univ.; Kimberly Dawn Kyker, Univ. Oklahoma; Brian Alan Maurer, Univ. Arizona; J. Michael Reed, Univ. Montana; Dan Alan Roberts, Univ. North Carolina—Charlotte; Mark Alan Shields, Univ. North Carolina—Wilmington; Steven Charles Sibley, Mississippi State Univ.; Douglas William White, Rutgers Univ.; Ann M. Wyckoff, Univ. North Dakota.

REPORT OF THE RESOLUTIONS COMMITTEE

The following resolutions were read during the second business meeting:
WHEREAS, humans and wildlife are equally dependent upon a healthy environment to maintain a quality existence, and

WHEREAS, the chlorinated hydrocarbon pesticides, endrin and heptachlor, are known to be acutely toxic and persistent in the environment, and

WHEREAS, the Compound 1080, or sodium fluoracetate, was banned in 1972 because of its non-selective toxicity to a broad range of wildlife other than the target species, and

WHEREAS, the field use of current pesticides, herbicides, and rodenticides cannot be limited to target species but must inevitably affect many interdependent forms of life, and

WHEREAS, the widespread use of such poisons is often promulgated by government agencies in preference to alternative and less hazardous control methods, and

WHEREAS, pesticides, herbicides, and rodenticides recognized as being so exceptionally hazardous to human beings that they are banned in the United States are still being manufactured for export to other countries, leading to both human and wildlife losses, and

WHEREAS, these losses of life should be a source of shame to all Americans.

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society urges President Ronald Reagan and the appropriate government agencies to:

(1) ban the field use of endrin and heptachlor in the United States;
(2) reinstate the Executive Order banning the use of Compound 1080 on federal lands (first signed by President Nixon in 1972 and upheld by every president thereafter) and also stop the registration of 1080; and
(3) halt the widespread shipment of DDT, Malathion, 2-4-D, 2-4-5-T, and other poisonous chemicals overseas where they may be used by people ignorant of the effects upon themselves, their children, and the wildlife about them.

WHEREAS, increasing evidence points to acid precipitation as a growing environmental problem in many parts of the United States, Canada, and Europe, and

WHEREAS, the problem is both national and international, with sources and affected areas seldom under the same governmental jurisdiction, and

WHEREAS, sufficient research has already been conducted to implicate acid precipitation as a major cause in the destruction of aquatic environments and higher forms of life.

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society urges the Congress of the United States to take a strong approach toward control of power plant emissions and other sources of air-borne acids before irreversible damage is done to the environment.

WHEREAS, Janet Hinshaw has shown dedication and hard work in her daily care and management of the Josselyn Van Tyne Memorial Library, and

WHEREAS, she has handled in an exemplary manner the library’s correspondence and mailing, its records, purchases, and sales, and many other aspects of related business for The Wilson Ornithological Society, and

WHEREAS, her care and dedication have been carried on in addition to her duties in the University of Michigan Museum of Zoology Bird Division and both jobs have been handled while raising two small children.

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society, on the occasion of its 64th Annual Meeting, salutes Janet Hinshaw, thanks her for almost 10 years of dedication, and hopes their happy association will continue for many years to come.

WHEREAS, The Wilson Ornithological Society has held its 64th Annual Meeting in Green Bay, Wisconsin, 2–5 June 1983, at the invitation of the University of Wisconsin–Green Bay, and

WHEREAS, we have enjoyed and benefitted from excellent facilities on this beautiful cam-
pus, warm hospitality from all concerned, a fine scientific program, and a wide array of field trips (with 5:30 a.m. hot coffee!) and other events.

Therefore be it resolved that the Wilson Ornithological Society expresses its gratitude and appreciation to Richard B. Stiehl and his local committee on arrangements, to Clait Braun, who organized the scientific program, and to the staff of the University of Wisconsin–Green Bay who helped to make our visit to Green Bay a pleasant and productive meeting.

PAPERS SESSION

The papers session was organized by Clait E. Braun. Sessions were chaired by Curtis Adkisson, Keith Bildstein, Clait Braun, Anthony Erskine, Abbot Gaunt, George Hall, Jerome Jackson, and Jon Barlow. A list of papers presented follows:

David G. Jennings, University of Georgia, "Estimating population size: a mark-recapture sampling of Red-tailed Hawks (Buteo jamaicensis)."

Jerome A. Jackson, Mississippi State University, "Aerial survey techniques for locating Red-cockaded Woodpecker colonies."

William W. Whitmar, II, University of Wisconsin–Green Bay, "Pre-nesting behavior of the Cactus Wren (Campylorhynchus bruneicapillus)."

Daniel R. Petit, The Ohio State University, "Avian nest orientation in response to predator surveillance and thermoregulation: a test of theory."

Harmon P. Weeks, Jr., Purdue University, "Why bridges?—A look at a bridge-nesting guild of birds."

Opal H. Dakin, Mississippi State University, "Nesting phenology and reproductive success of European Starlings in Mississippi."


Keith L. Bildstein, William S. Clark, David L. Evans, Marshall Field, Len Soucy, and Ed Henckel, Winthrop College, "Fall migration of Northern Harriers in eastern North America."

Helmut C. Mueller, University of North Carolina–Chapel Hill, "The evolution of reversed sexual dimorphism (RSD) in Falconiformes: hypotheses and data."

Robert W. Storer, University of Michigan, "The source of feathers eaten by grebes."

Richard L. Knight, University of Wisconsin–Madison, "Responses of nesting ravens to different levels of human activity."

Margaret C. Brittingham and Stanley A. Temple, University of Wisconsin–Madison, "A comparison of vegetation around parasitized and nonparasitized nests within deciduous forest habitat."

Carol A. Corbat and Richard H. Yahner, The Pennsylvania State University, "Effects of habitat patchiness created by small clear-cuts on Rufous-sided Towhees and Gray Catbirds."

John R. Probst, USDA Forest Service, "Kirtland's Warbler habitat suitability."

Daniel S. McGeen, Pontiac, Michigan, "Kirtland's Warbler update."

Stanley A. Temple, University of Wisconsin–Madison, "An allelochemical antipredator mechanism in the Mauritius Pink Pigeon."

Shonah A. Hunter, Southern Illinois University, "Age determination using aspartic acid enantiomers."

Nancy S. Mueller, North Carolina Central University, "Blood transfusions aid skin graft retention in Mallard ducklings."
James L. Ingold, Miami University, “Endangered species of cranes: electrophoretic determination of relationships.”

Terry P. Wiens and Francesca J. Cuthbert, “Status of the Piping Plover (Charadrius melodus) in Lake of the Woods, Minnesota.”

T. A. Sordahl, Luther College, “Does the downy American Avocet mimic the adult Wilson’s Phalarope?”


Francesca J. Cuthbert, University of Minnesota–Duluth, “The effect of garter snake (Thamnophis s. sirtalis) predation on Common Tern (Sterna hirundo) reproductive success.”

Sandra L. L. Gaunt, The Ohio State University, “The Borror Laboratory of Bioacoustics: a resource in transition.”

George B. Reynard, Riverton, New Jersey, “A rarely heard vocalization of an adult Turkey Vulture (Cathartes aura).”

Karen Marie West, University of Wisconsin–Madison, “Response of vocal, inconspicuous waterbirds to playback recordings at Horicon Marsh.”

Gary Ritchison, Eastern Kentucky University, “Variation in the songs of female Black-headed Grosbeaks.”


Susan K. Knight, University of Wisconsin–Madison, “Daily activities of White-tailed Ptarmigan during the breeding season.”

Clait E. Braun and Kenneth M. Giesen, Colorado Division of Wildlife, “Winter home range size of White-tailed Ptarmigan.”

Robert J. Small, Wisconsin Cooperative Wildlife Research Unit, “Mortality and dispersal of Ruffed Grouse in central Wisconsin.”

Cathy C. Blohowiak and P. B. Siegel, Virginia Polytechnic Institute and State University, “Mate preferences of Japanese Quail as influenced by plumage color.”

T. David Pitts, University of Tennessee at Martin, “Use of small and large nest boxes by Eastern Bluebirds.”

**ATTENDANCE**

**COLORADO:** Ft. Collins, Clait E. Braun.

**DISTRICT OF COLUMBIA:** Washington, James Tate.

**DELWARE:** Greenville, David Niles.

**FLORIDA:** Gainesville, Mary H. Clineh.

**GEORGIA:** Athens, David Jennings.

**IOWA:** Cedar Falls, Peter Lowther; Cedar Rapids, Harlo Hadow; Decorah, Tex Sordahl.

**ILLINOIS:** Carbondale, Shonah Hunter, Eugene LeFebvre; Elgin, Dave Brinker; Macomb.

Ed Franks; Springfield, Carl Becker.

**INDIANA:** West Lafayette, Harmon Weeks.

**KENTUCKY:** Richmond, Gary Ritchison.

**LOUISIANA:** Metairie, Cecil Kersting.

**MARYLAND:** Frostburg, Robert Paterson.

**MICHIGAN:** Ann Arbor, Robert W. Storer; Cedar Grove, George Allez; Grand Rapids, Mary Whitmore; Jackson, Robert Whiting; Pontiac, Dan McGeen.

**MINNESOTA:** Cass Lake, Lowell Suring; Duluth, Francesca J. Cuthbert, P. B. Hoflund.

Terry Wiens; Minneapolis, Thomas Van Hof; St. Paul, J. R. Probst, H. B. Tordoff.
MISSOURI: Kansas City, Karen Holmes.
NORTH CAROLINA: Chapel Hill, Kenneth O. Horner, Helmut Mueller; Durham, Nancy Mueller; Wilmington, James Parnell.
NEW JERSEY: Riverton, George Reynard.
NEW YORK: Ithaca, Susan Norvell; Lansing, Helen Lapham.
OHIO: Columbus, Abbot S. Gaunt, Sandra L. L. Gaunt, Daniel Petit, Kenneth Petit, Lisa Reichhardt; Gambier, Robert D. Burns, James Caley; Oxford, James Ingold; University Heights, Bruce McClean.
PENNSYLVANIA: Kemptown, Stan Senner; University Park, Carol A. Corbat.
SOUTH CAROLINA: Chester, Mrs. W. C. Stone.
SOUTH DAKOTA: Vermillion, Byron Harrel.
TENNESSEE: Martin, David Pitts.
TEXAS: Victoria, Christine Mitchell, Donald White.
VIRGINIA: Blacksburg, Cathy Blohowiak, Curtis Adkisson; Scottsville, Linda Whiteside.
WISCONSIN: Baraboo, Scott Hereford; Coloma, Bob Small; Fond du Lac, Ronald Barrett; Green Bay, Steve Coleman, Theresa A. Duffey, Thomas Erdman, John Link, Richard B. Stiehl, Le Wenger, William Whitmar, Jennifer Zellner, Gregg Zuberbier; Madison, Margaret Brigham, Ann Marie Francis, Silvia Halkin, Richard Knight, Susan Knight, Stanley A. Temple, Karen West; Manitowoc, Charles Sontag; Menasha, Mike Minock; Menomonee, Richard Wilson; Milwaukee, Edward Burkett, Thomas W. Carpenter, Shan Duncan, Millicent Ficken, Robert W. Ficken, Elmer W. Strehlow, Gwyn Tuttle, Charles M. Weise; Plainfield, Frances Hamerstrom, Frederick Hamerstrom; Randolph, Charles Gilmore; Trego, Kate Engel; West Bend, Noel J. Cutright.
WEST VIRGINIA: Bethany, Albert Buckelew; Morgantown, William Hall.
NEW BRUNSWICK, CANADA: Sackville, Anthony J. Erskine.
ONTARIO, CANADA: Toronto, Jon C. Barlow, Margaret L. May, Deron May Barlow.
AUSTRALIA: Brisbane, Douglas Dow.

1984 ANNUAL MEETING

The Sixty-fifth Annual Meeting of The Wilson Ornithological Society will be held at the University of North Carolina-Wilmington, from 31 May–2 June 1984. The University is host for the meeting, to be held concurrently with the Annual Meeting of the Carolina Bird Club. There will be a scientific program, field trips to many interesting sites, workshops of interest to amateur and professional ornithologists, and a spouses’ program. Dr. James F. Parnell is chairman of the Committee on Local Arrangements. His address is Department of Biology, University of North Carolina-Wilmington, Wilmington, North Carolina 28401.
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By Mary C. McKittrick

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