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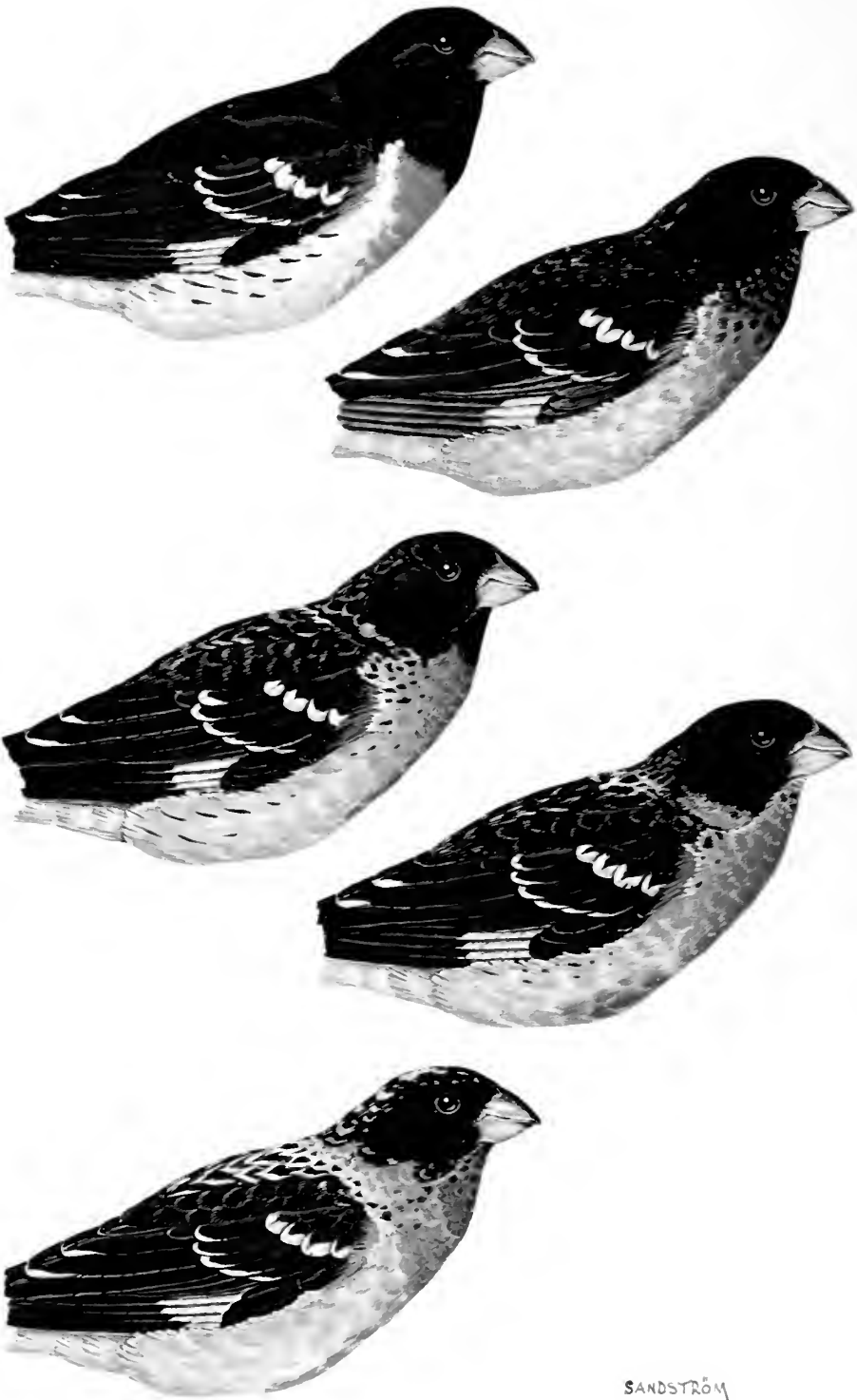
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SANDSTRÖM

Hybrid male grassbeaks (*Pheucticus ludovicianus* X *P. melanocephalus*)
from Gregory County, southeastern South Dakota.
Painting by George Sandström.

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CHARACTERISTICS AND REPRODUCTIVE BIOLOGY OF GROSBEAKS (*PHEUCTICUS*) IN THE HYBRID ZONE IN SOUTH DAKOTA

BERTIN W. ANDERSON AND RAYMOND J. DAUGHERTY

The Rose-breasted Grosbeak (*Pheucticus ludovicianus*) breeds widely in the eastern United States and the Black-headed Grosbeak (*P. melanocephalus*) in the west. The two forms are sympatric and hybridize in the Great Plains (West, 1962; Kroodsma and Cassell, 1968), an area where several additional eastern and western bird taxa also interbreed (Sibley and West, 1959; Sibley and Short, 1959, 1964; Short, 1965; Kroodsma and Cassell, 1968; Rising, 1970; Anderson, 1971). The characteristics of grosbeaks in the hybrid zone in South Dakota have not previously been reported, nor have such details as the kinds of pairs formed, clutch size, viability of eggs, and nesting habitat. The purpose of this report is to document hybridization in South Dakota as well as to present data on the above aspects of reproductive biology.

Grosbeaks are common breeding birds along rivers and streams supporting relatively dense vegetation in South Dakota (Fig. 1). This riparian vegetation is dominated by cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and box elder or river maple (*Acer negundo*). This habitat connects breeding areas of grosbeaks in eastern and western South Dakota and is where hybridization occurs.

Six rivers, all of which eventually enter the Missouri River, extend from west to east in western South Dakota (Fig. 1). Riparian vegetation along them becomes less luxuriant to the westward, as the result of drier conditions and heavy grazing—the latter being especially significant in preventing the development of an understory. Perhaps largely for these reasons grosbeaks are scarce westward along these tributaries. Woodlands along the Missouri River itself were formerly important links between eastern and western populations, but reservoir construction initiated in the 1950's has greatly reduced habitat. Consequently, contact between eastern and western populations of woodland birds is now limited along that river (Anderson, 1971).

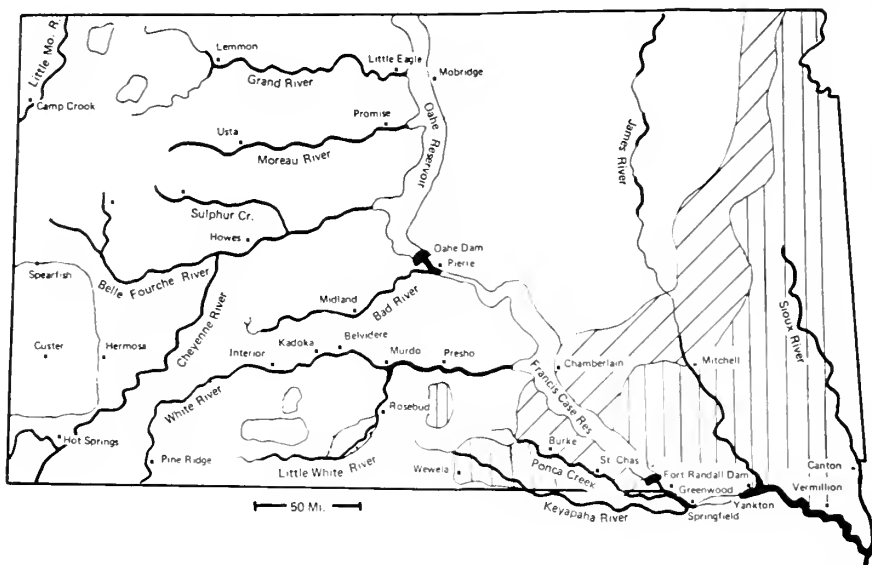


FIG. 1. Collecting localities and vegetation in South Dakota. Clear areas indicate treeless plains; irregular shaped patches, ponderosa pine (*Pinus ponderosa*); vertical lines, farm groves and shelter belts; and diagonal hatching, areas transitional between treeless plains and farm groves. Wooded portions of rivers and streams are shown by heavy lines, non-wooded portions by light lines.

CHARACTERISTICS IN THE OVERALL HYBRID AREA

This aspect of our study, based on 469 specimens (now housed at the James Ford Bell Museum of Natural History, University of Minnesota), documents the degree as well as the extent of hybridization. Preceding this analysis we collected males throughout much of the state (Fig. 1; also see Table 3) in late May, June, and early July 1965-68. An effort was made to collect all males encountered in order to obtain as nearly random a sample as possible. As some hybrid characters are rather subtle and difficult to discern in the field, the chance of an unintentional bias favoring the collecting of hybrids was further reduced. A hybrid index was established using the criteria in Table 1. In that

TABLE 1
COLOR CHARACTERS AND SCORES USED TO ASSESS THE EXTENT OF HYBRIDIZATION

| Males | Score |
|--|-------|
| Nape | |
| Black as in <i>P. ludovicianus</i> | 0 |
| Black with buffy-brown traces | 1 |
| Buffy-brown neck collar as in <i>P. melanocephalus</i> | 2 |

TABLE 1. *Continued*

| Males | Score |
|--|-------|
| Back | |
| Black as in <i>P. ludovicianus</i> | 0 |
| Black with some brown streaks | 1 |
| Broad brown streaks as in <i>P. melanocephalus</i> | 2 |
| Rump | |
| White as in <i>P. ludovicianus</i> | 0 |
| Mixed brown and white | 1 |
| Brown as in <i>P. melanocephalus</i> | 2 |
| Flanks | |
| White as in <i>P. ludovicianus</i> | 0 |
| Mixed white and brown | 1 |
| Brown as in <i>P. melanocephalus</i> | 2 |
| Breast and underwing coverts | |
| Rose as in <i>P. ludovicianus</i> | 0 |
| Slightly orange or salmon pink | 1 |
| Orange | 2 |
| Salmon yellow | 3 |
| Chrome yellow as in <i>P. melanocephalus</i> | 4 |
| Total | 0-12 |
| Females | Score |
| Throat, breast, and side of neck | |
| Buffy-white as in <i>P. ludovicianus</i> | 0 |
| With traces of fawn-brown | 1 |
| Fawn-brown with traces of buffy white | 2 |
| Rich fawn-brown as in <i>P. melanocephalus</i> | 3 |
| Extent of yellow | |
| If present restricted to underwing coverts as in <i>P. ludovicianus</i> | 0 |
| Traces of yellow on head and/or breast | 1 |
| Yellow superciliary line and on breast as in <i>P. melanocephalus</i> | 2 |
| Streaking | |
| Relatively wide brown streaks over most of ventral surface as in <i>P. ludovicianus</i> | 0 |
| Similar to above but streaks fewer and somewhat narrower | 1 |
| Streaking reduced and streaks narrower | 2 |
| Streaks narrow, absent over much of ventral surface as in <i>P. melanocephalus</i> | 3 |
| Total | 0-8 |

TABLE 2
INDEX SCORES OF BREEDING GROSBEAKS (*PHEUCTICUS*) FROM OUTSIDE THE
ZONE OF INTERGRADATION

| | Males | | | | Females | | | |
|-----------------------------|-------|------|-----------------|--------------|---------|------|-----------------|---------------|
| | N | Mean | Percent scoring | | N | Mean | Percent scoring | |
| | | | 0 or 12 | 1-2 or 11 | | | 0 or 8 | 1-2 or 6-7 |
| <i>P. ludovicianus</i> | 72 | 0.2 | 85 | 15 | 65 | 0.2 | 78 | 22 |
| <i>P. m. melanocephalus</i> | 125 | 11.8 | 86 | 14 | 29 | 7.3 | 63 | 37 |

index "pure" *P. ludovicianus* scores 0 and "pure" *P. melanocephalus* 12 in males and 8 in females.

In testing this index, we also analyzed variation in grosbeaks from outside of the zone of intergradation. In 291 such specimens (Table 2), we found scores duplicating weak hybrids in 14 and 15 percent of eastern and western males, respectively, and 22 and 37 percent of eastern and western females. Because of the low scores and mosaic distribution of this "hybridity," we regard it more as an intrinsic form of variation than due to introgression. As for its bearing on indices in the area of hybridization, it simply means that low scores of hybridity are of less significance than higher ones.

In the analysis of South Dakota specimens, subadult and adult males have been combined, as they had nearly identical values. Female age classes were not evident and overall indexing of this sex was more subjective and prone to error than that of males. This may have had some slight effect on our results and conclusions. A detailed description of the two forms and an alternative method of scoring them has been presented by West (1962).

The major area of hybridization was northwest of Greenwood, Charles Mix Co., where the male hybrid scores and number of intermediate hybrids (scores 4-8) were greater than at any other locality (Table 3). In the 12 miles from that locality to the one southeast of Greenwood, the hybrid incidence decreased by nearly half and the number of intermediate hybrids to about a fourth. Another significant shift in populational (male) phenotypes occurred in the 12 miles between St. Charles and Burke, Gregory Co. The Burke population was dominantly of *P. melanocephalus* (score 12), compared to the one at St. Charles being closer to *P. ludovicianus* (scores 0-2). Westward from Greenwood a marked decrease also occurred in the proportion of intermediate hybrids as the proportion of *P. melanocephalus* increased. Further study of the westerly situation was precluded as grosbeak habitat is virtually absent along the Ponca Creek and Keyapaha River west of Burke.

In a sample of 106 specimens collected along the White, Bad, Grand, and Little White Rivers (Fig. 1), 98 were "pure" *P. melanocephalus*. Only seven hybrids, all phenotypically similar to *P. melanocephalus* (scores 10-11), were

TABLE 3
CHARACTERISTICS OF MALE GROSBEAKS COLLECTED IN THE AREA OF HYBRIDIZATION
IN SOUTH DAKOTA

| Localities and distances between localities | Sample size | Percentages in various phenotypic categories | | | |
|---|-------------|--|-----------------------------------|----------------------------------|--|
| | | Pure <i>P. ludovicianus</i> (score 0) | Intermediate hybrids (scores 4-8) | Other hybrids (scores 1-3, 9-11) | Pure <i>P. melanocephalus</i> (score 12) |
| Vermillion 30 mi. | 82 | 87 | 0 | 13 | 0 |
| Yankton 40 mi. | 44 | 77 | 0 | 23 | 0 |
| Springfield 12 mi. | 53 | 58 | 6 | 36 | 0 |
| se Greenwood 12 mi. | 36 | 61 | 6 | 30 | 3 |
| nw Greenwood 15 mi. | 76 | 28 | 21 | 42 | 9 |
| *Spencer 15 mi. | 13 | 46 | 15 | 23 | 15 |
| St. Charles 12 mi. | 35 | 29 | 11 | 34 | 26 |
| Burke | 24 | 4 | 9 | 33 | 54 |

* Totals not equaling 100 percent resulted from rounding off.

collected: at Belvidere (1), on the White River; at Pierre (4), on the Missouri River; and at Midland (2), on the Bad River. The only "pure" *P. ludovicianus* collected was at Rosebud on the Little White River. This series of populations, formerly linked with eastern ones along the Missouri River, is now disjunct due to reservoirs that have eliminated intervening habitat.

CHARACTERISTICS AND BREEDING BIOLOGY OF MATED PAIRS

This phase of the study was based on 110 presumed mated pairs (now housed at the American Museum of Natural History). These were collected in 1969-72 in the area of greatest hybrid incidence, that is, northwest of Greenwood. Birds were presumed paired if they were both observed at or usually within 10 feet of the same nest. Because grosbeaks are highly territorial, encroachment of a "foreign" bird this close to a nest is unlikely and was not known to have occurred in this study. Thus these pairs are presumably genuine.

Randomness of pairing.—A test of the randomness of pairing was made by using a 3×2 contingency table composed of the male scores 0-2, 3, and

TABLE 4
PHENOTYPIC COMBINATIONS IN MATED PAIRS (COLLECTED)

| Male index values | Female index values | | | | | | | | | Total pairs |
|-------------------|---------------------|----|----|---|---|---|---|---|---|-------------|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| 0 | 10 | 11 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 28 |
| 1 | 10 | 8 | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 29 |
| 2 | 6 | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 13 |
| 3 | 4 | 4 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 13 |
| 4 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| 5 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| 7 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 12 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 9 |
| Totals | 39 | 34 | 28 | 2 | 3 | 1 | 1 | 1 | 1 | 110 |

4-12 and the female scores 0-1 and 2-8. These categories are the maximum number allowable when following Remington and Schork's (1970) suggestion that no expected frequency be less than 1 and not over 20 percent be less than 5. The results of analysis suggest that the sampled pairs (Table 4) approximated combinations expected in a randomly interbreeding system ($0.10 > P > 0.05$). Both members of the pair were hybrid in 64 percent of the cases. It is perhaps significant that both of the relatively pure *P. melanocephalus* females (scores 7-8) were paired with "pure" *P. melanocephalus* (score 12) males.

Clutch size and egg viability.—Data concerning clutch size and egg viability were obtained for 70 of the 110 mated pairs. In nests containing only eggs, an egg was considered viable if there was no evidence of a dead embryo or of a lack of development (when siblings did show development). The use of these procedures gave conservative estimates of mortality up to hatching.

Mean clutch size for hybrid females (scores 2-6) did not differ significantly from year to year. On the other hand "pure" females (scores 0-1 or 7-8) had significantly smaller clutches the first two years of the study ($X = 2.8$, $N = 8$) than the last two ($X = 3.8$, $N = 35$). This difference is probably misleading, as four excluded clutches found during the first two years

TABLE 5
DISTRIBUTION OF PHENOTYPES IN SUB-HABITAT TYPES (SEE TEXT)

| Male index scores | Sample size | Percent in sub-habitat | | | | Female index scores | Sample size | Percent in sub-habitat | | | |
|-------------------|-------------|------------------------|----|-----|----|---------------------|-------------|------------------------|----|-----|-----|
| | | I | II | III | IV | | | I | II | III | IV |
| 0-3 | 87 | 45 | 21 | 18 | 16 | 0 | 46 | 24 | 17 | 13 | |
| 4-8 | 12 | 41 | 25 | 29 | 9 | 1-2 | 53 | 17 | 20 | 12 | |
| 9-12 | 11 | 82 | 0 | 9 | 9 | 3-8 | 11 | 45 | 9 | 18 | 27* |

* Total less than 100 percent due to rounding off.

of the study each had at least 3 eggs and possibly 4 or 5 eggs. They were excluded because precise clutch size information could not be obtained. If one assumes that these 4 nests had a mean clutch of 3.5 eggs, the overall mean would be 3.0 and significance of the difference (at the 0.05 level) would be lost. In the absence of more convincing evidence that clutch size varied from year to year we have combined the clutch sizes from all years to facilitate comparisons of hybrids and non-hybrids.

Pairs in which the female was essentially pure (scores 0-1 or 7-8) had 3.6 eggs per nest with 9 non-viable among 153 eggs (5.9 percent). Pairs in which the female was hybrid (scores 2-6) had 3.0 eggs per nest with 8 non-viable among 81 eggs (9.9 percent). A two-tailed z-test of the mean clutch sizes reveals that the difference is statistically significant ($z = 2.35$, $0.02 > P > 0.01$), with clutch size lower in hybrids.

Subadult and adult males were associated with clutches of nearly identical size. Phenotypically, the male of pairs with clutches of 1, 2, or 3 eggs was as likely to be a pure individual as a hybrid. The two pairs with "pure" *P. ludovicianus* females (score 0) and *P. melanocephalus* males (scores 11-12) had clutches of 4 and 5 eggs.

Habitat.—We distinguished four sub-habitats in the locality northwest of Greenwood. The first (I) was more or less continuous dense woods with relatively dense understory. The second (II) included areas similar to this but which were relatively small isolated stands. The third (III) included woods in which cattle grazed, which markedly reduced the understory. The final sub-habitat (IV) was a campground in which the trees were more spaced and an understory was totally lacking.

Males indexed as *P. ludovicianus* or intermediate (scores 0-8) and all females showed an approximately similar proportional distribution among the sub-habitats (Table 5), this being an average for the males of 46, 20, 18, and 16 percent, respectively for sub-habitats I, II, III, and IV. On the other hand, 9 of 11 *P. melanocephalus*-like males (scores 9-12) were found in

TABLE 6
SUB-HABITATS (SEE TEXT) IN WHICH MATED AGE CLASSES OF MALE GROSBEAKS
WERE FOUND

| Sub-habitat | Sample size | Percent | |
|-------------|-------------|---------|-----------|
| | | Adult | Sub-adult |
| I | 53 | 85 | 15 |
| II | 21 | 43 | 57 |
| III | 20 | 75 | 25 |
| IV | 16 | 69 | 31 |

the denser woods with well-developed understories, and the respective percentages were 82, 0, 9, and 9 for the sub-habitats. Although this difference is statistically significant (Chi-square 4.1; $P < 0.05$), the number of such males collected is small and we have little faith in the result. Furthermore, 10 of the 11 *P. melanocephalus*-like males were adults, and this age class prefer the denser, more luxuriant areas (Table 6). Subadults were significantly more abundant in the less luxuriant areas (Chi-square 5.6; $P < 0.02$).

Trees selected for nesting.—Fifty-nine percent of the nests occurred in box elder, which constituted only 30 to 40 percent of the trees in any area. Ash, American elm, and cottonwood were about equally abundant, but these held only 8 percent of the nests. The same general preference for nesting sites seemed to be shown by all phenotypes.

Height of nest.—Nearly 70 percent of the nests were between 10 and 19 feet above the ground. Eight of the 10 nests occurring over 20 feet high were in habitats with poorly developed understories. In sub-habitats with a well developed understory (I and II) 33 percent of 55 nests were 15 feet or more above the ground, whereas in sub-habitats with a poorly developed understory (III and IV) 61 percent of 31 nests were 15 feet or more above the ground. There was no apparent association between phenotype and height of nest.

Cowbird parasitism.—Cowbird eggs and/or young were found in 16 of 70 nests (22.9 percent) with completed clutches. There was a tendency toward increased cowbird parasitism as the index value of the male of the pair increased. Three of the 6 nests in which the male of the pair was similar to *P. melanocephalus* contained at least one cowbird egg.

DISCUSSION

Although analysis suggests that pairing is random, some assortative mating cannot be entirely precluded. The fact that 78 percent of the 9 hybrid females

(scores 3-8) were mated with hybrids (scores 2-11) or *P. melanocephalus* (score 12) males, even though this group of males included only 48 percent of the sample, suggests some assortative mating. Further, both female *P. melanocephalus* (scores 7-8) were mated with "pure" *P. melanocephalus* (score 12). West (1962) also found *P. melanocephalus* females mated to males of the same species more frequently than might be expected by chance alone.

If *P. melanocephalus* females prefer males of the same species, as the data suggest, one might suppose that some females were unmated in the population northwest of Greenwood. In that locality 12 percent of the mated males were phenotypically like *P. melanocephalus* (scores 9-12), but only about two percent of the mated females were similar to *P. melanocephalus* (scores 7-8). *P. ludovicianus* females apparently accepted any male as a mate, but possibly a scarcity of acceptable mates existed for *P. melanocephalus* females.

Westward from Greenwood the hybrid incidence decreased, perhaps because more male *P. melanocephalus* were in the population and available to such females. This may have forced more of the female *P. ludovicianus* to mate with males of their own species or with hybrids. In other words, assortative mating by female *P. melanocephalus* could be operating, thus keeping the two taxa from achieving a more concerted hybridization.

West (1962) found that in Nebraska the zone of intermediacy was about 100 miles wide. His data show a gradual clinal gradation from one morphotype to the other. In South Dakota, the zone of intermediacy is less than 70 miles wide and the cline apparently much steeper. Major shifts in population structure occurred over distances as little as 12 miles (Table 3), as already explained.

West (1969) concluded that the grosbeaks should be considered conspecific in the absence of any reproductive isolation. We disagree with his conclusion because we found (1) a steep cline of intergradation, with hybrids most numerous in a narrow zone at the periphery of the ranges of the two forms, (2) some evidence of assortative mating, and (3) some evidence of reduced viability among hybrid females. Furthermore, we did not find a true zone of hybridization, that is, an area where pure parental phenotypes occur only in numbers that likely result from genetic recombination or immigration (Short, 1969). We found that hybridity was never above 63 percent, which means that one parental type or the other constituted at least a third of any population.

These lines of evidence suggest that the grosbeaks do not interbreed freely, and when they do interbreed, it is not without penalty. The steep cline within the zone of intermediacy in South Dakota suggests that the gene pools of these two morphotypes have acquired a degree of mutual incompatibility.

that is, counterselection is occurring. Taxonomically, we agree with Hubbard (1969) that where the evidence suggests both the existence of gene flow and the operation of counterselection, a semispecies designation should be applied. Semispecies have attributes of both species and conspecies (Mayr, 1963), and this term applies to the relationships of *P. ludovicianus* and *P. melanocephalus*. Together the two constitute a superspecies. This conclusion is in agreement with Short (1969) and Mayr and Short (1970). Amadon (1966), Hubbard (1969), and Short (1969) have offered suggestions concerning the nomenclatural recognition of semispecies taxa.

SUMMARY

Hybridization between *Pheucticus ludovicianus* and *P. melanocephalus* was studied in South Dakota. The greatest numbers of hybrids were found in populations along the Missouri River near the Nebraska-South Dakota border. A shift from largely *P. ludovicianus*-like male phenotypes to largely hybrid phenotypes occurred abruptly over a 12 mile distance from Springfield to Greenwood. Within another 40 miles to the west occur reductions in *P. ludovicianus* and in intermediate hybrids, with *P. melanocephalus* becoming the predominant phenotype. An analysis of mated pairs revealed that pairing did not deviate significantly from that expected in a randomly interbreeding system, but there was some evidence that *P. melanocephalus* females prefer to mate with males of the same morphotype. Hybrid females had significantly smaller clutches. We concluded from the above and from other evidence that these grosbeaks constitute semispecies and together are superspecies.

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NEW LIFE MEMBER



Thomas Henry Foster is now a Life Member of The Wilson Ornithological Society. He is a member of several nature-connected organizations and is a free-lance writer. His hobbies are nature-observing and gardening, and his travels have taken him to Eurasia and Africa. He has published many reviews in The New York Times Book Review section and his ornithological interests center on behavior. He lives in Bennington, Vermont, and is married.

THE FIRST PREBASIC MOLT OF THE YELLOW-BREASTED CHAT

ALLAN R. PHILLIPS

Ornithologists long ago noticed the occurrence of molt in the outer primaries of young Yellow-breasted Chats (*Icteria virens*). From this fact, they not illogically concluded (starting with Dwight, 1900:282) that the first prebasic (postjuvinal) molt in this species is complete. As they found no evidence of molting remiges in the young of any other North American parulids (purported exceptions discussed later), the idea developed that this molt separated *Icteria* from all the other genera. Together with its exceptional behavior, bill shape, and mouth color, this led to justifiable doubts as to whether the genus belongs in the Parulidae or in some other family.

By now, the supposed "complete postjuvinal molt" of the Yellow-breasted Chat has become all but legendary. It is cited in such a standard work as Bent (1953:590) and it continues to appear in more recent papers, such as Ficken and Ficken (1962). Blake (1962) calls it "now well established."

The present paper proposes to reopen the question of the completeness of this molt and to assess its possible taxonomic and other significance.

MATERIALS AND METHODS

For years, in connection with studies of migration routes and dates, I have routinely collected warblers, in Arizona and at times elsewhere, from mid-August on into the autumn. Age was determined whenever possible by direct examination of the skull and, in females, also by the condition of the ovary. In addition, a series of *Icteria v. virens* netted in Veraacruz in September 1965, in connection with virological studies, was kindly made available to me in the flesh by Dr. Robert W. Dickerman, to whom I express my gratitude.

THE MOLTS OF *ICTERIA*

In my limited collecting in spring, I have found no evidence of any regular prealternate (prenuptial) molt in the Yellow-breasted Chat. This is in agreement with the findings of previous workers. Thus the summer aspect or breeding plumage, which hardly differs from that of winter, is achieved entirely by wear.

In Arizona and Sonora, at least, the prebasic (postnuptial) molt of adults seems to take place on or near the breeding grounds. This may be true of the species generally, as of so many Parulidae. At least, I have no evidence of worn or molting chats, of any race (or age), at a point distant from the breeding areas. In some chats the molt continues into early October.

The same general principles apply to young. Not unlikely these scatter

more than adults, as a natural consequence of adult territoriality and youthful inquisitiveness. It is also likely that there is a wider spread in the dates of molting, depending on those of hatching. Some young, presumably birds that hatched late, still wear considerable amounts of juvenal plumage into mid-September. They doubtless molt into October.

Careful examination of young chats ($n = 30^{\pm}$) in late summer and early fall, shows that, with one possible exception, the molt is *not* complete. Usually the four innermost primaries in each wing are retained from the juvenal plumage. The number varies to some extent, ranging from 3 to 6. In one case, Dickerman and I found a young female *I. v. virens*, now Delaware Mus. Nat. Hist. 26458, which had indeed molted most or all of its primaries—certainly at least the outer 7. This is an exceptional case, and I suspect that some late-hatched birds may molt no primaries at all. This pattern of molt is true of both *I. v. virens* and of Arizona *I. v. auricollis*.

Whether or not the secondaries are normally molted is more difficult to ascertain. These remiges, protected by the overlying tertials, do not fade and wear so quickly, nor are they as easily studied in dried skins. Furthermore, the problem of whether immature chats molt the rectrices remains unsolved. Those I have examined appear to have retained them. The tertials, however, seem to be molted. Examination of more young chats in late summer is needed, particularly of individuals that are in the midst of their primary molt.

MOLT AS AN AID TO AGE DETERMINATION

This molt pattern affords a new method for determining the age of chats in fall, winter, and, to some extent, later. A freshly-molted adult has a relatively uniform wing. All the primaries are about the same color and texture—dusky and unworn. The outer (9th) primary is usually shorter than the 4th, which is decidedly longer (2, commonly 2.5, to 3 mm) than the 3rd; this in turn is often 2 mm longer than the 2nd. Usually primaries 3, 4 and 5 show a steady, almost even progression of increased length in both wings. The difference in length between any primary and the next is seldom more than 2.0 times the immediately preceding difference.

Fall immatures, on the other hand, usually show a definite break where the darker, fresher, less brownish outer primaries begin. In at least one wing there will be a difference of 3 to 7 mm between the innermost (shortest) fresh outer primary and the outermost (longest) old inner one. This difference is $2\frac{1}{2}$ to 5 times that between the outermost old primary and the adjacent longest old primary. In adults the difference between this set of primaries is rarely more than 4 mm. In addition, the 9th primary in immatures is usually about as long as the 4th, or even a bit longer. In adults, as

mentioned above, it is usually shorter. (One must, of course, check for broken or missing primaries.)

As wear progresses through winter and spring, the somewhat subtle color difference of the primaries usually disappears. Even so, less-than-one-year-old birds are often recognizable by the abrupt gap, in at least one wing, between the gradual gradient of length of the inner primaries and the abrupt gradient of the outer ones.

Of course, the usual skull differences (degree of "ossification") are also useful in early fall. In late September and early October most young still have the skull largely or wholly unossified, and narrow anterior or median "windows" persist in the few November-December immatures I have seen. Some probably retain windows into January, but I have no proof of this. At any rate, I seriously question the statement of Dennis (1967:134) that by 2 December "all Chats regardless of age" would probably have ossified skulls. The specimen reported by him should be reexamined in accordance with the above molt criteria.

I am much less confident of the usefulness of mouth-color in age determination. The black mouth of breeding males is a *seasonal* development. In early fall they still show traces of dusky, but these possibly vanish later. Adult females in fall may still show a little black in the inside of the upper mandible or maxilla, but this is chiefly limited to the distal median part.

TAXONOMIC CONSIDERATIONS OF MOLT

Three other wood warblers have been stated or implied to have complete first prebasic molts. Of these, the Common Yellowthroat (*Geothlypis trichas*) has already been restudied by Ewert and Lanyon (1970): they found no evidence of such a molt. Dennis (1958) also reported such a molt in the Pine Warbler (*Dendroica pinus*), as well as mentioning another case of a juvenile chat that "had nearly completed the tail molt." Dwight (1900), on the contrary, found this molt incomplete in *D. pinus*, as have I in the few juveniles examined: I suspect that Dennis was in error in reporting the molt to be otherwise. Finally, there is the purported case of a complete first prebasic molt in the Yellow-rumped Warbler (*D. coronata*), mentioned in Phillips et al. (1946). A complete body molt was intended, indeed and implied—as the passing mention of "a complete prebasic molt" occurs in the discussion of seasonal variation in coloration, i.e. body plumage. At any rate, to my definite knowledge, only *Icteria* among the young of North American Parulidae actually regularly molts any of its primaries.

What other songbirds, then, do show a first prebasic molt approaching that of *Icteria*? This pattern is more or less regular in shrikes (*Lanius*), occurring in species of both New and Old World (Philippines, at least). It

is also found in most species of *Passerina* buntings, including "*Guiraca*" *caerulea* at least occasionally (i.e. Delaware Mus. Nat. Hist. 13113). I do not, however, find evidence of it in Rosita's Bunting, *P. rositae*.

Since it is most unlikely that *Lanius*, *Icteria*, and *Passerina* have any real relationship, I can only conclude that molt patterns do not elucidate the taxonomy of *Icteria*. More promising are anatomical data such as those of Beecher and George (*in* Eisenmann, 1962:267).

SUMMARY

Despite ideas to the contrary, the first prebasic molt of the Yellow-breasted Chat is incomplete and of doubtful taxonomic importance; but it does afford a valuable clue for age determination, even into the following spring or summer.

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EGG-NEGLECT IN THE WILSON'S STORM PETREL

JAIME E. PEFAUR

The purpose of this study was to determine the frequency and duration of egg-neglect periods and their influence on nest temperatures in Wilson's Storm Petrel (*Oceanites oceanicus*). The study was done on Robert Island, South Shetland, Antarctica. The island, largely ice-covered, has been described by Schlatter et al. (1968) and by Pefaur and Murua (1972). The so-called Robert Island peninsula is a narrow western extension about 2 km in length and 200 to 500 meters in width. Physiographically, the peninsula is a plateau averaging about 30 to 40 meters above sea level, but with some elevations up to 80 meters; a narrow beach surrounds the plateau. Mean summer temperature is between 0° and 2.5°C, and the peninsula becomes ice-free.

Nesting species of birds there include *Macronectes giganteus*, *Daption capensis*, *Catharacta skua*, *Larus dominicanus*, *Sterna vittata*, as well as *Oceanites oceanicus*. *Pygoscelis antarctica*, *P. papua*, *P. adeliae*, *Phalacrocorax atriceps*, and *Chionis alba* have been recorded as non-breeding visitors (Pefaur and Murua, 1972). The storm petrel population was estimated in 1969 as between 1,000 and 2,000 individuals (Pefaur and Murua, 1972), dispersed in 13 nesting colonies on the peninsula. Nests were placed 20 to 50 cm deep inside rock crevices and were cup-shaped, made of mosses and lichens, with an average diameter of 6 cm and depth of 1 cm.

On the Argentine Islands, Graham Land, Roberts (1940) recorded temperatures of burrows occupied by incubating *O. oceanicus* and found that temperature remained above that of the ambient air. The burrows there were covered with a rich layer of mosses and lichens, in marked contrast to the more usual situation as found on Robert Island, where the nests were placed in naked rock crevices. Nest temperature thus dropped drastically as soon as the incubating bird left in the latter locality.

METHODS

Selection of study nests was very difficult for they were dispersed in a large area and well hidden. Furthermore, the nests had to be relatively close to our temporary headquarters in order that they could be checked every six hours, in all weather. The three nests selected were on a north-facing slope, in burrows which were not so deep as to hide them. From 15 January to 22 February 1969, nests were checked at 6:00, 12:00, 18:00, and 24:00 hours every day. A #408 probe was initially placed under the egg in the adults' absence, and connected by 50 meters of lead to a fixed thermistor (Yellow Springs Instrument Company, Dayton, Ohio). Ambient air temperature was recorded at the thermistor, using a #405 probe. Nesting behavior of the petrels was not altered by this

TABLE 1
DURATION OF BROODING AND EGG-NEGLECT PERIODS IN *OCEANITES OCEANICUS* ON ROBERT ISLAND, SOUTH SHEETLAND ISLANDS, ANTARCTICA*

| Unsuccessful (Nest 1) | | Successful Nests | | | |
|--------------------------|----------|------------------|---------|----------------|---------|
| Period (in hours) of | | (Nest 2) | | (Nest 3) | |
| Brooding | Neglect | Brooding | Neglect | Brooding | Neglect |
| 12 | 84 | 36 | 30 | 60 | 6 |
| 36 | 48 | 36 | 6 | 72 | 48 |
| 60 | 36 | 54 | 18 | 66 | 42 |
| 90 | 6 | 6 | 12 | 18 | 18 |
| 48 | 18 | 54 | 42 | 18 | hatched |
| 12 | 12 | 198 | 18 | — | — |
| 42 | 30 | 12 | 36 | \bar{x} 48.8 | 28.5 |
| 42 | 12 | 78 | 18 | | |
| 24 | 18 | 120 | hatched | | |
| 6 | deserted | — | — | | |
| — | — | \bar{x} 66.0 | 22.5 | | |
| \bar{x} 37.2 | 29.3 | | | | |

* All observations begun January 16.

procedure. Dates on which incubation was initiated were, unfortunately, unknown in all cases; however, in all three nests incubation was well underway.

RESULTS

Periodic egg-neglect during incubation was known to occur in *O. oceanicus* in Graham Land (Roberts, 1940), and it occurred in the three nests studied by me (Table 1). Nest 1 had nine periods of egg-neglect (before the nest was abandoned), averaging 10.1 hours/day. Nest 2 had eight egg-neglect periods, averaging 5.4 hours/day, and nest 3, at a more advanced stage, had only four egg-neglect periods, averaging 7.6 hours/day. The longest periods of neglect were 84 hours for nest 1, 42 hours for nest 2, and 48 hours for nest 3.

Every time a bird left the nest and was not replaced immediately by its mate, the nest temperature quickly dropped to ambient air temperature (Fig. 1). Every major trough in the nest temperature curve represented an absence of a brooding bird. On the other hand, each time the nest temperature exceeded 10°C corresponded with a sitting bird. No definite patterns of egg-neglect could be seen in the data. Periods of neglect followed as soon as 6 hours after the previous period of neglect and as long as 198 hours after such a period.

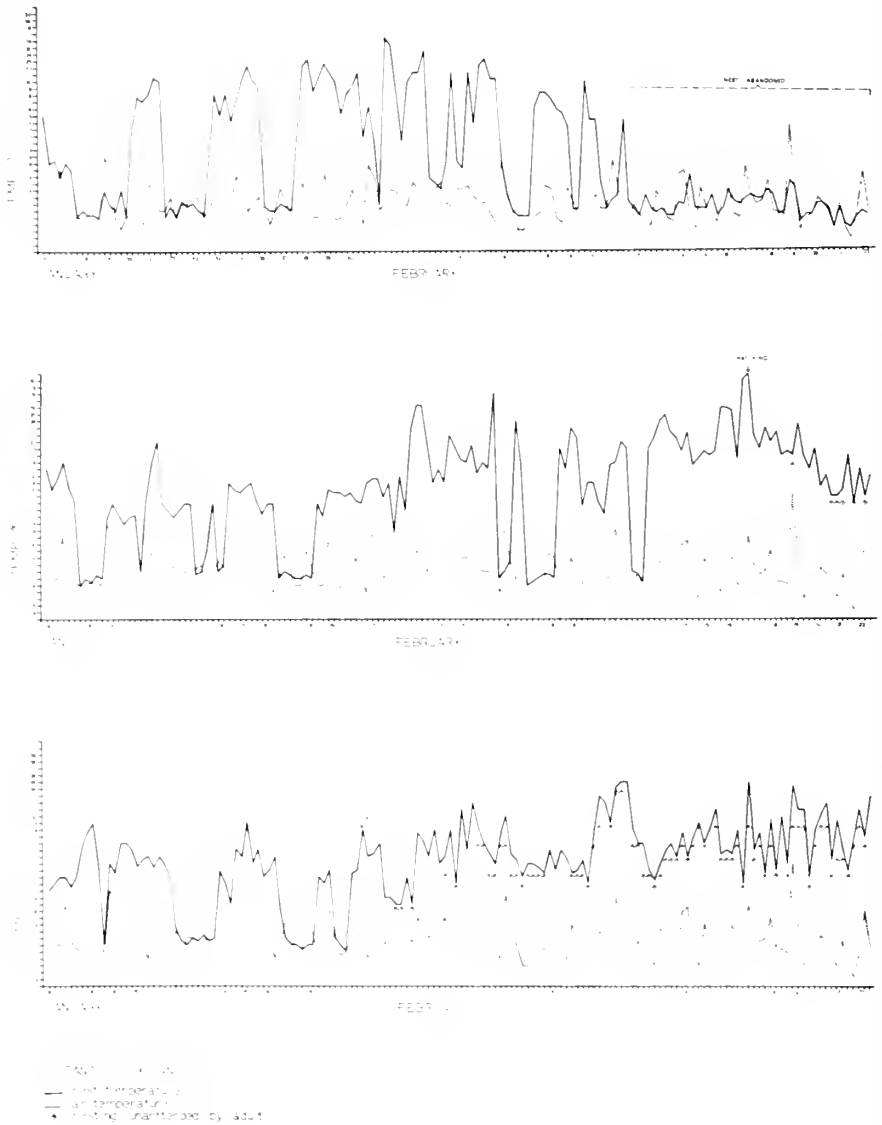


FIG. 1. Nest temperatures in three nests of *Oceanites oceanicus* on Robert Island, South Shetland, Antarctica. Nest 1 (upper graph) was abandoned, but nests 2 and 3 (middle and bottom graphs, respectively) successfully hatched chicks.

The temperatures recorded by the thermistor probe are actually somewhat lower than the incubation temperature of the embryo. Westerskov (1956) found in *Phasianus* that the temperature on the upper surface of incubated eggs was about two to ten degrees higher than the lower surface. Drent (1967) recorded nest bottom temperatures of 27°–35°C, but internal egg temperature was constant at 39°C. In *Puffinus* and *Diomedea* internal egg temperatures are about 36°C (Howell and Bartholomew, 1961a, b). Although not reflecting actual incubation temperatures, there is no reason to suppose that the thermistor values for nest temperature do not also indicate that the eggs were affected.

Following hatching, a parent brooded the nestling for the first 48 hours in nest 2, and for 36 hours in nest 3. Subsequently, the chick was left alone an increased number of times (Fig. 1). Body temperature of the newly hatched chick is low, Roberts (1940) having recorded it as 25° and 27°C in unattended chicks during their first day of life. Later a body temperature is attained which fluctuates about 37°C; body temperature in petrels is fully discussed by Warham (1971).

DISCUSSION AND CONCLUSIONS

Temporary suspension of incubation and concomitant periods of egg-neglect have been recorded for many Procellariiformes. The species listed in Table 2 are known to hatch successfully subsequent to chilling periods. Many more species (i.e. *Daption capensis*, *Pagodroma nivea*, *Pterodroma phaeopygia*, *Puffinus lherminieri*, *Halobaena caerulea*, *Calonectris diomedea*, and *Oceanodroma leucorhoa*; from several sources) are known to have periods of egg-neglect, but there is no information on subsequent successful hatching. In the incubation periods of some circumpolar species, where the temperature sometimes reaches freezing, the egg can be chilled for up to two days and still hatch afterwards, as the present study affirms.

It is possible that egg-neglect may have evolved as opportunistic behavior on the part of Procellariiformes that modifies the length of the incubation period, with the result that the chick leaves the nest when food is most abundant (Prévost and Bourlière, 1955). Maher (1962) found that timing of fledging in Snow Petrels (*Pagodroma nivea*) was an adaptation permitting "the recently fledged juveniles to encounter a maximum food supply in their early period of independence," and suggested that several breeding features of Procellariiforms are correlated with a mid-April peak in the standing crop of Antarctic zooplankton.

It is still necessary to establish when the first egg-neglect period occurs in the *O. oceanicus*: the present data were recorded only in the last two-thirds of the incubation period, which extends from November to March on Robert

TABLE 2
EGG-NEGLECT PERIODS IN PROCELLARIIFORMES AT NESTS IN WHICH SUCCESSFUL
HATCHING OCCURRED

| Species | Egg-neglect Period (days) | Source |
|--|---------------------------------|------------------------------|
| <i>Diomedea immutabilis</i> , Laysan Albatross | 4 to 5 | Hadden, 1941 |
| <i>Diomedea upomophora</i> , Royal Albatross | 2 | Richdale, 1952 |
| <i>Pterodroma macroptera</i> , Great-winged Petrel | 1 | Warham, 1956 |
| <i>Pachyptila tartur</i> , Narrow-billed Prion | 1 | Richdale, 1965a |
| <i>Pachyptila desolata</i> , Dove Prion | 1 to 2 | Tickell, 1962 |
| <i>Procellaria puffinus</i> , Manx Shearwater | 1 to 7* | Matthews, 1954 |
| <i>Puffinus griseus</i> , Sooty Shearwater | 4** | Richdale, 1963 |
| <i>Pelagodroma marina</i> , White-faced Storm Petrel | 1 to 4 | Richdale, 1965b |
| <i>Oceanites oceanicus</i> , Wilson's Storm Petrel | 1 to 2 | Roberts, 1940 |
| <i>Hydrobates pelagicus</i> , Storm Petrel | 1 to 5 | Lockley, 1932 Davis, 1957 |
| <i>Fregatta tropica</i> , Black-bellied Storm Petrel | 1 | Beck and Brown, 1971 |

* "Clearly the seven days survived by an egg in the burrow is not the limit of the resistance to chilling, because others remained viable for up to 13 days in the laboratory" (Matthews, 1954).

** Thought to be due to the investigator disturbance (Richdale, 1963).

Island. It is possible that in the first third of the period the embryos have different resistance to chilling. However, in the Manx Shearwater (*Puffinus puffinus*), the stage of development at which chilling occurs seems unimportant (Matthews, 1954).

SUMMARY

Frequency and duration of egg-neglect periods in *Oceanites oceanicus* were studied on Robert Island, South Shetland, Antarctica. Of three nests observed, two successfully hatched young, even though they experienced four and eight periods of egg-neglect before hatching, averaging 7.6 and 5.4 hours day, respectively. Longest periods of egg-neglect were 42 and 48 hours. Body temperature of newly hatched chicks was 25°-27°C. Prolonged egg-neglect may be common in Procellariiformes, and may modify the length of the incubation period so that the chick fledges when food is most abundant at sea.

RESUMÉN

Este estudio se llevó a cabo en la Isla Robert, Shetland del Sur, Antártica, durante la XXIII Comisión Antártica Chilena. El objetivo principal fue para establecer la frecuencia de los abandonos del nido durante la incubación de *Oceanites oceanicus* y ver cuales eran sus consecuencias. Tres nidos fueron estudiados y en dos de ellos hubo eclosión del huevo despues de varios abandonos sufridos. Este abandono temporal parece ser un comportamiento bastante difundido entre los Procellariiformes, y sería el un comportamiento

oportunitico a objeto de modificar la lonitud del periodo de incubación con lo cual se logra que, al momento de abandonar esos lugares, los polluelos de este petrel encuentren abundante alimento en el mar mientras realizan su primera migración.

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PRODUCTIVITY, POPULATION DYNAMICS, AND
SYSTEMATICS OF GRANIVOROUS BIRDS

This book, edited by S. C. Kendeigh and J. Pinowski and published by the Polish Academy of Sciences, Warsaw (410 pp., 1973), may be obtained from Dr. S. C. Kendeigh, Vivarium Building, Wright and Healey Streets, Champaign, Illinois, 61820, for \$13.00, plus \$.60 for postage and handling (total \$13.60). The book covers the Proceedings of the First General Meeting of the Working Group on Granivorous Birds of the International Biological Program held at the Hague, Holland, September 6-8, 1970. The major subjects discussed are (1) Bioenergetics, (2) Population dynamics and related aspects of behavior, (3) Food, in relation to the primary production of cereals and weeds—economic aspects, (4) Systematics and evolutionary biology of sparrows, and (5) Miscellaneous problems. Altogether there are 31 separate papers authored by 43 persons from 16 countries. Two species of common birds receive principal attention, the House Sparrow and European Tree Sparrow, but consideration is also given to a number of other species so that principles brought out have application to birds in general.

COPULATORY BEHAVIOR OF DOWNY WOODPECKERS

LAWRENCE KILHAM

Study of the courtship of woodpeckers might be regarded as being in its infancy, as much remains to be done in showing how, in terms of evolution, patterns of courtship and pair bonds interrelate with feeding habits and a bird's total way of life. This point of view, discussed elsewhere in relation to the White-breasted Nuthatch (*Sitta carolinensis*) (Kilham, 1972a) and recently described by McKinney (1973) as ecoethology, is elaborated further in the final discussion of this report in relation to both Hairy (*Dendrocopos villosus*) and Downy (*D. pubescens*) Woodpeckers.

All aspects of the courtship of a species have to be studied in detail if ecoethology is to have meaning. This appears to be particularly true of the copulatory behavior of Downy Woodpeckers, which appears to be a unique performance and to have a special importance in promoting the pair bond as well as attachment to the nest site. That copulation in woodpeckers can have an important role beyond its ordinary one of reproduction has also been recognized by Short (1971).

Present studies were carried on mainly in Lyme, New Hampshire, between 1961 and 1973; 72 copulations were observed, mainly in three pairs whose nest sites were well-suited for observation.

Other accounts of the reproductive behavior of *D. pubescens* include those of Bent (1939), Staebler (1949), and Lawrence (1967), of which the latter two give descriptions of copulations. I have encountered no comprehensive account of the copulatory behavior, nor statement concerning the hover approach (described later) as being a unique performance. The main displays and vocalizations of Downy Woodpeckers are given in Kilham (1962).

DESCRIPTION OF COITION

Invitation pose of female.—When ready for copulation a female Downy Woodpecker may fly to the male, perching crosswise or occasionally lengthwise on a horizontal limb (Fig. 1), raise up on her legs with, to shorten a description by Lawrence (1967), "her tail pointing straight out, her head up and tilted backward, her . . . breast thrown out, her wings slightly dropped and motionless." This performance results in an outline more like that of some passerine species, a fact also noted by Steinfatt (1937) for the female of the Great Spotted Woodpecker (*D. major*).

Hover approach of male.—The male landed on the back of the female following a hovering approach in all of the observed copulations. An example illustrating the main features of these hovers is as follows:



FIG. 1. Copulatory behavior of the Downy Woodpecker showing the flight and hover of the male as well as the invitation pose of the female.

On 6 May 1971 Male B was resting on a horizontal branch close to the nest hole when the female flew to him. He immediately moved until he was 30 cm away from her and facing in an opposite direction, then launched himself in a slow, hovering flight, turning in the air when in a position about 60 cm below and 1.3 m behind his mate (Fig. 1). From here, still hovering and almost stationary, he slowly rose until he was slightly above her and landed on her lower back. Copulation then followed, the hover preceding it having taken about 2 seconds.

Configuration of branches and tree trunks where the female took her invitation pose might alter the pattern of the approach as well as of copulation. A feature was that the male often moved away from his mate when she flew to him, sometimes moving as much as 75 cm, as though he needed room to maneuver in launching his aerial approach. Lawrence (1967), in a description of the hover, states that the male "left his perch and on rapidly beating wings hovered above (the female) for about 5 seconds." In the approaches I have witnessed the male reached a point above the female only at the very end of his performance, and hovering lasted only 2 seconds.

Two aspects of the hover are worthy of emphasis. One is that it possibly is unique for *D. pubescens*, as I have not encountered description of it for

any other woodpecker species, including the similar-sized European Lesser Spotted Woodpecker (*D. minor*). Hovering is found in other groups of birds, Hinde (1954), for example, describing it in detail for the Green Finch (*Chloris chloris*). The second aspect of the hover is that the male Downy Woodpecker acts almost as if repelled by the female. Thus, as I saw repeatedly, if the female flew close to him to assume the copulation pose, he would move away rather than toward her. It is conceivable from this point of view that the hover flight evolved from this initial repulsion. By the deliberate hover and approach from the rear, taking appreciable time, a male may be able to overcome his initial aversion to physical contact.

It is curious that Staebler (1949), who describes eight copulations of *D. pubescens*, makes no mention of the hover approach. One wonders, therefore, whether he failed to notice it or whether this behavior occurs in some parts of the species range and not others. Staebler mentions one male as fluttering on the back of a female, but such fluttering can be seen with many species of woodpeckers (as well as other birds) when a male, off balance, seeks to stabilize himself.

Coition.—Once mounted on the back of the female, the male Downy, like the males of other species of woodpeckers (Lawrence, 1967; Blume, 1963; Kilham, 1959, 1966a) falls gradually to the left. During this time his tail is moved under that of the female and at the time of cloacal contact is turned forward to lie along her right side. The male meanwhile holds his balance by spreading both wings. His right wing may lie across the lower back and tail of his mate while his left one rests against the branch where she is perching. The period of close contact is held for a seemingly long time. I have timed it as ranging from 10 to 16 seconds both with a wrist- and a stopwatch: Lawrence (1967) gives timings of 14 and 18 seconds and Staebler (1949) of 12–15 seconds. The male, while thus more or less inverted, is usually looking upward and moving his head about. This is in contrast to the Hairy Woodpecker (*D. villosus*) which, as Lawrence (1967) has also noted, may lie so both male and female have their heads nearly in parallel and are looking in the same direction.

Abortive coition.—At times the male may mount the female as in full copulation, but once mounted, both birds fall away within a few seconds, suggesting either one or both is not in sufficient readiness. In 1971 I saw seven abortive copulations in the same period as 24 full copulations and in 1972 five abortive copulations to 15 full copulations.

CIRCUMSTANCES ATTENDING COPULATION

In studying Pair B, I visited the nest stub every day except one between 6 May and 22 June 1971, spending on an average an hour in the morning

and a half hour in the afternoon on week days and almost twice this time on weekends. Trees in the swamp were low and bare of obstructing foliage throughout much of May. Details of circumstances attending copulations were as follows:

Location.—All of the 24 copulations noted for the swamp pair took place within 7 m, and usually less, of the nest hole, which was 10 m above the swamp. Most of them, i.e. 17 of the 24, occurred on a favored "copulation" branch that extended within 9 m of the entrance. The male, spent much of his time within a short flying distance of the nest stub, and I had no evidence of copulatory activity occurring elsewhere in periods of observation. All of the 72 copulations noted for a total of 3 pairs of *D. pubescens* took place close to the nest, as is also described by Lawrence (1967) and Staebler (1949). This would seem to be a feature of the copulatory behavior of this species, even though I might have missed some copulations taking place elsewhere. I have not observed any such constant relation in *D. villosus* (Kilham, 1966a and MS) and Short (1971) notes that only a few of the copulations he observed in Nuttall's (*D. nuttalli*) and Ladder-backed (*D. scalaris*) woodpeckers occurred in the proximity of nest sites. Pynnönen (1939), on the other hand, states that most of the copulations of the Greater Spotted Woodpecker (*D. major*) take place near the nest, where the two sexes meet most often. He also noted that copulations often took place on a definite branch.

Time of day and frequency.—The copulations of Pair B were noted at all hours from 06:30, which was within 10 minutes of the time the male emerged from roosting, until 17:40: 13 of the 24 were in morning hours, a time of greater activity also noted by Pynnönen (1939) for *D. major*. The greatest frequency was at the time of egg-laying. On 11 May, for example, copulation at 10:45 was followed by a second one only 2 minutes later, and a third one, following an abortive attempt, at 11:10. This spate of copulations in a 25-minute period was exceeded 4 days later, on 15 May, when three copulations took place in the 17 minutes between 06:48 and 07:05. On the following day copulation at 07:32 was followed by another 2 minutes later. I timed these two as lasting 14 and 10 seconds respectively. Considering that on most days I was only by the nest at hour and half hour periods, the total number of copulations per day must have been well beyond the recorded numbers. Pynnönen (1939) states that *D. major* may copulate six times a day in the egg-laying period.

Invitation to copulation.—Copulations may be initiated by either the male or the female. In many cases the two birds seemed in equal readiness, the precipitating circumstance being that both were by the nest at the same time. Between copulations, or several of them occurring close together, only a

single bird, usually the male, remained near the nest. The range of circumstances preceding copulations were as follows:

(i) In the first days of the copulation period (6–8 May), MB would be excavating while his mate, who did almost none of the work, was away. I seldom saw FB except when she came for copulation. If her mate was within the nest hole, she would fly to it directly, then fly to the copulation branch to take her invitation pose when he looked out. On occasions when MB was already out of the hole, at times preening in leisurely fashion on the copulation branch, the female would still fly to the hole before coming to him. This initial flight to the nest is also described by Shuster (1936) for the Lesser Spotted Woodpecker. He considered it an important link in the chain of copulatory behavior and, as in the case of *D. pubescens*, this aspect of the behavior of the female suggests that copulatory behavior, among other purposes, serves to strengthen emotional attachment to both nest and mate.

(ii) Female B was apparently laying eggs from 11 to 18 May, hence she was by the nest hole more than previously. She had been able to enter the hole readily before this time, but during this period had difficulty. She would bow in and out of the hole, on occasions 12 to 15 times, before being able to force her way in, possibly due to an increase in body size when carrying an egg. She also spent much time resting below the hole. When her mate, who always stayed away when she was by the nest, flew in and alighted on the copulation branch, she would then fly to him to copulate. It thus seems that initiation of copulation might be by either sex, according to the phase of nesting.

(iii) Either bird might drum in seeking copulation as also noted by Staebler (1949). On 8 May FB drummed for 3 minutes about 20 m from the nest stub, then she flew to the hole and from there to the preferred branch for copulation. On 16 May, after finishing the nest excavation and before the onset of incubation, the male spent much time idling by the nest, as he often did in the interim. After 50 minutes of this he drummed for several minutes, at 10:25 and again at 10:36. His mate flew in after the second drumming and copulation followed. A similar sequence had occurred the day previously, shortly after the male emerged from roosting at 06:45. During his periods of idling the male gave occasional “whinnies.” As noted for other pairs, “whinnies” are given by both sexes, but especially by the male during the period of copulations, although not associated with them as directly as the drummings.

Behavior following copulation.—There was no set behavior following copulation. In the period 6–8 May the male often returned to the hole to continue excavating and in the period 11–18 May, that of egg-laying, the female might fly to rest below the entrance. On two occasions she remained on the copu-

lation branch, still perching crosswise, and the male returned within 2 minutes for a second copulation. At other times the female moved to a tree trunk nearby. I twice saw the male hovering close to her as she shifted about the trunk. Either after such an episode or soon after copulation, the female might fly off with the male in pursuit.

Lawrence (1967) also mentions this pursuit flight. She describes the female as inviting the male to follow. Another interpretation, suggested by the behavior of Pair B, was that in some instances the female might be satiated while the male still had an urge to copulate. He might then hover seeking further contact with the female. When she failed to respond, the male may have been expressing instincts in the pursuit flight. In this respect the pursuit flights of the White-breasted Nuthatch (*Sitta carolinensis*) (Kilham, 1972a) appear, to be similar in nature to those of *D. pubescens*.

Copulatory activity during incubation.—Incubation in Pair B began on 18 May, and although I saw no copulations on that day, I did see one each day on the 19th, 21st, and 22nd. The last one was thus on the fifth day of incubation, after which copulatory behavior was sporadic and fragmentary. On 25 May the male drummed when coming to the nest then alighted on the copulation branch. His mate, meanwhile, flew out from the nest hole and took an invitation pose on the branch, but flew off before he had a chance to hover. On the following day, the ninth of incubation, the male chased her in a pursuit flight after a roughly similar episode. The last of the fragmentary type of behavior was seen on 29 May, close to the time of hatching.

Lawrence (1967) states that copulatory behavior declines first in the female. This was not evident with Pair B, however, as the partners appeared to lose interest more or less simultaneously. Pynnönen (1939) similarly noted in *D. major* that once incubation had begun, the male at one time and the female at another might be ready for copulation when its mate was not. He also found, as I did for *D. pubescens*, that the last full copulations of *D. major* and *D. minor* took place five days after incubation had begun.

OTHER ASPECTS OF COPULATORY BEHAVIOR

Copulation with an intruder.—On the morning of 9 May FB fell from a tree in spasm, apparently due to retention of an egg as described elsewhere (Kilham, 1972b). I took her home before returning her, still essentially helpless, to the swamp an hour later. I saw no more of her until 11 May. By the afternoon of the day she disappeared (9 May) a female (NF) with very different head markings had arrived by the nest. A feature of her behavior during the two days of her stay was that she began an excavation of her own in a stub 7 m from the nest and worked at it periodically and without interference from male MB. NF hitched up his nest stub twice while

I was watching. Each time MB attacked and drove her away. He was otherwise tolerant of her presence. On 9 May, not long after being chased away, NF took an invitation pose on a nearby branch and I saw MB hover. Copulation probably followed, but I was not in a position to see well. On the next day, at 10:45, I watched a full copulation under much the same circumstances. NF remained in position after the male had left. He returned and mounted her again in an abortive copulation. NF then circled his nest stub, but when within 20 cm of the hole, the male not only attacked but also pursued her in a long flight. I saw no more of NF on following days when FB had returned.

Lawrence (1967) gives description of a somewhat similar episode. In her case the females of two adjacent pairs were laying eggs when one of them was killed. The still-mated female had to pass through the territory of the newly unmated male to reach a feeding station, and while doing so she stopped on a branch near his nest stub, took an invitation pose, and copulation followed. A case of promiscuity is also mentioned by Staebler (1949).

Notably in Pair B, although MB was willing to copulate with the new female, he was quick to drive her away from his nest and hence did not accept her as a mate. This jealous attachment to the nest appears to illustrate the crucialness of the cavity to the pair bond of *D. pubescens*. The fact that all or nearly all copulations took place in its vicinity may well have served to strengthen this attachment.

The new female, NF, was evidently in search of a mate in association with a nest hole. Unable to visit the hole already constructed, she had an immediate urge to set about excavating another close by. The willingness of the male to copulate with the intruder, in this case as in that of Lawrence, is understandable in view of the male's peak of sexual readiness.

Loss of nest and effect on copulations.—In 1972 pair B excavated a nest cavity 60 m from where they had nested the year before. I saw a first abortive copulation on 6 May and a full copulation at 16:45 on the following day. MB did almost all of the excavating which he largely completed by 11 May. Although I saw 4 copulations between 13 and 17 May, MB, contrary to his behavior of the year before, did not remain by the nest hole. It was an unusually cold spring and it seemed probable that a general lack of insect life gave little inducement to start nesting. His absence left the hole unguarded, and a pair of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) that he had driven away repeatedly on other days, took over the nest cavity. They quickly enlarged the entrance on 18 May until it was no longer suitable for the Downy Woodpeckers. By the next day MB was exceedingly active in looking for a new nest site. In spite of the absence of a definite nest site, copulatory behavior of MB and FB continued. At 07:30, for example, MB had started

a trial excavation in stub No. 1 when FB flew to him and copulation followed. By 09:47 MB had started trial excavation in stub No. 2, when his mate flew to him as before and copulations followed on a nearby branch. It was apparent from these episodes that a completed nest cavity was not needed for copulation to occur, and I was also to observe such behavior in a following year. MB tried five different sites before finally selecting one on 19 May. He worked incredibly hard on 19 and 20 May, seeming to complete most of the work those two days, with little time taken off for feeding. In spite of this pace, copulation continued. Each time, FB initiated the copulation by flying to a branch close to the excavation and he then flew to her. The last copulations seen were on 24 May.

Early copulatory behavior.—Although the period of daily copulations does not begin until a nest is nearing completion, several observations made in 1973 indicated that isolated copulations can occur at the start of excavations. On 2 May, for example, I found Male C with just his head in a hole recently begun: and later abandoned his mate flew to a branch nearby and a full copulation followed. In 1968 I had noted a similar situation, with two copulations in 4 minutes on 27 April by a site later abandoned by the pair. A third example of early copulation was with Pair D. On 6 May 1973 Male D was still working on his outside nest hole when his mate came near and the two had an abortive copulation. My wife and I watched the nest for 2 to 4 hours daily for the next 2 weeks. We saw no further copulations until 10 May, and then witnessed them almost daily, with 21 the total reached by 21 May.

EXPERIENCE WITH A HAND-RAISED PAIR

I raised a brood of Downy Woodpeckers in an aviary in 1959, and in the following year a pair of them excavated a nest hole. On 28 April the female started taking invitation poses, but the male showed little sign of readiness until 1 May when he mounted in an effort at copulation. He did not use the hover approach and as he mounted he fell off to the right. On 5 May he again copulated in similar fashion. None of the five eggs subsequently incubated by both Woodpeckers was fertile.

From this one might conclude that the male *D. pubescens* may not be sexually mature in his first nesting season, a situation also noted for *D. villosus* (Kilham, 1966a). If the aviary Downy was indeed sexually immature, he may not have yet acquired complete copulatory behavior, including the hover approach and falling to the left. Lawrence (1967) noted that "the act (coition) requires no little skill on the part of the male. Young and inexperienced males often show that the movements are not altogether innate but are to some extent learned. Some individuals at times display distinct

TABLE 1

COMPARATIVE BREEDING AND COPULATORY BEHAVIOR, BASED ON 72 COPULATIONS NOTED FOR THE DOWNY AND ON 49 FOR THE HAIRY WOODPECKER IN NEW HAMPSHIRE

| Activities of Paired Males (M) and Females (F) | <i>D. pubescens</i> | <i>D. villosus</i> |
|--|------------------------|---|
| Vocalizations on meeting— | “Chirr” | “Joick, joick” “tewk, tewk” |
| character— | Harsh | Exuberant |
| Travel together in feeding | Seldom; well separated | Frequent (for a part of each day) |
| Supplanting attacks M on F | Frequent | Infrequent (away from feeders) |
| Tapping by potential nest hole | Relatively seldom | Frequent |
| Onset copulatory behavior | May | February-March |
| Copulations | Duration | 13-16 seconds |
| | Character | M first moves away, then flies as to approach F from rear; hovers |
| | Location | Close to nest excavation (within 15 m) |
| | | 6-10 seconds |
| | | M ascends trunk and moves out along branch directly to F. |
| | | No flight or hover |
| | | Close to nest 22 times, away from nest 27 times |

bewilderment and hesitation . . .”. Along these lines she describes an inexperienced male that hopped along a branch to the female, with no hover, and “twice . . . hesitated, recoiled, then again advanced, as if something in the situation were radically wrong. Finally he reached her, mounted, tramped on her back, still hesitating, then swung himself under her tail—but lost his grip and fell off.” Both birds on separating, resorted to displacement pecking.

Both Lawrence’s observations and my own thus support a concept that the complete copulatory behavior, while basically innate, is something the male has to learn as well.

DISCUSSION

Although the courtship and copulatory behavior of Hairy Woodpeckers has been described in Kilham (1966a), many additional observations made since that then have gone into the summaries shown in Table 1. The breeding activities listed there for *D. villosus* are all suggestive of a close pair bond. To a human observer a pair of that species appears to enjoy each other’s company with relatively little repulsion to physical contact, as indicated by copulatory activity beginning in February, and to have a pair bond tied in

with the nest site but not to the extent seen in *D. pubescens*. In almost every activity listed in Table 1, Downies differ from Hairy Woodpeckers. One's impression of *D. pubescens* is of a mild repulsion operative between the members of a pair, in the female possibly through fear of the male and in the male through his aggressiveness in supplanting attacks. The nest cavity, chiefly excavated by the male as also noted by Lawrence (1967), is the center of the copulatory activity which, in being the chief and almost the only form of courtship, and thus serves a dual function.

The Heinroths (1958) have stated that "many . . . woodpeckers are not particularly fond of their mates." While this statement does not apply to such species as the Hairy, the Pileated (*Dryocopos pileatus*), and the Crimson-crested (*Campyphilus melanoleucos*) Woodpeckers (Kilham, 1959a, 1966a, 1972c), to cite a few examples, it does appear to apply to the Black-backed (*Picoides arcticus*) (Kilham, 1966b), Downy, and, to judge from descriptions given by Bock (1970), Lewis' (*Asyndesmus lewis*) Woodpeckers.

One may wonder why the breeding and courtship behavior of two similar plumaged, sympatric species such as *D. pubescens* and *D. villosus*, should be so remarkably different. The matter of maintaining reproductive isolation may be only a partial answer. Natural selection, according to Mayr (1963), is always a compromise, and from this point of view the breeding behavior of a species is tied in with its total economy. This basic difference between Downy and Hairy Woodpeckers relates to bill size and feeding habits. From observations made in New Hampshire, it has seemed to me that *D. villosus*, in having evolved sexual differences in feeding behavior (Kilham, 1965), as well as a strong bill to dig out larger wood-boring larvae, can survive well in winter on its breeding territory. The ample food supply gives Hairy Woodpeckers a margin of leisure in winter that can be devoted to courtship. In this respect, as discussed elsewhere (Kilham, 1972a), they resemble the sympatric White-breasted Nuthatches, which also begin breeding behavior in January and February.

These situations are very different for *D. pubescens*. Its winter food supply, at least in Lyme, New Hampshire, appears to be marginal. Individuals seldom remain on their breeding territories in winter, as Lawrence (1967) has also noted for Canada. In some winters a number concentrate where food is locally prevalent, as on paper birches (*Betula papyrifera*) infested with the coccid *Xylococcus betulae* (Kilham, 1970). Even there, Downy Woodpeckers appears to need all daylight hours to find enough prey to survive. In a more closely competitive situation, males make relatively frequent supplanting attacks on females. This leads to a spacing out of the sexes, with males feeding on the upper part of the birches. While this leads to a more efficient

utilization of resources, the aggressiveness of the males and the need to feed steadily all day do not favor any early onset of breeding behavior. The margin of leisure needed for full courtship depends on a relatively abundant food supply. For *D. pubescens* this does not come until May with the emergence of new populations of insects that it can obtain by gleaning. By this time the pair has formed and a nest site has been selected and largely excavated by the male. Up until this time the members of a pair continue to spend a minimum of time together, as in winter. This situation changes when the completion of the nest hole coincides with the onset of warmer weather, as it usually does. Copulatory behavior then begins and serves, in addition to its strictly reproductive function, as the main form of courtship.

SUMMARY AND CONCLUSIONS

Downy Woodpeckers appear to have a unique form of copulatory behavior in which the male may first move away from a soliciting female, then fly to approach her from the rear in a hovering flight.

Successful copulations last 13-16 seconds, which is relatively long in comparison with those of the related, sympatric Hairy Woodpecker.

Copulations may take place many times a day, over a 2-week period that may extend from the end of nest excavation up to the fifth day of incubation. These may be preceded by a few copulations at the very beginning of an excavation.

All of the 72 copulations observed at this time took place in the vicinity of the nest cavity, attachment to which appears to be tied in closely with the pair bond in *D. pubescens*.

Several unusual incidents were noted. In one of these a female was absent for 2 days, and an intruder female immediately took her place. Although the intruder copulated with the male, the male would not allow her to come close to the nest.

In a second incident, the nest cavity was taken over by sapsuckers at the beginning of the copulatory period. The copulations of the pair of Downies continued nonetheless, the female flying to wherever the male was excavating in his varied search for a new nesting site.

The members of pairs of *D. pubescens* are relatively antagonistic to each other during much of the early breeding season, with almost none of the intimate vocalizations and displays observable in the courtship of *D. villosus*. Under these circumstances copulations appear to serve as a comparatively important form of courtship as well as having a strictly reproductive function.

In both *D. pubescens* and *D. villosus*, patterns of courtship appear to have evolved in close relation to the feeding behavior of winter and spring months; differences in the total economy of each species accounting for differences, among other things, of the nature of their pair bonds.

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PLAY IN HAIRY, DOWNY, AND OTHER WOODPECKERS

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There is room for disagreement as to just what constitutes play among lower animals. Although clearcut definitions appear to be avoided by many ethologists, a number of generalizations presented by Marler and Hamilton (1967) are apposite to the present report. In discussing play behavior, for example, these authors state that "observers agree on the subjective judgment that lack of 'seriousness' is a key quality." This lack of seriousness was also a quality in observations I have referred to as play. In each case the woodpeckers were performing, whether in the field where I have been observing them on a year-round basis for 16 years, first in Maryland and then in New Hampshire, or in aviaries where I have studied hand-raised woodpeckers of eight species for a total of eight years, in a manner that strongly suggested that their activities were serving no immediate function and were done at times when the birds were idle with nothing pressing to do.

Marler and Hamilton continue "that individual acts observed in play are often similar to those recurring in normal versions of the same major pattern." For purposes of convenience the play behavior described below can be placed under three headings, namely, agonistic, courtship, and food-storing, each involving a major pattern.

PLAY VERSIONS OF AGONISTIC BEHAVIOR

In my observations I have noticed two forms of play that were agonistic (defensive) in nature. One form of play, in the field as well as in the aviary, was a lively dodging and shifting around the trunk of a tree with wings extended backwards (Fig. 1), with a Black-capped Chickadee (*Parus atricapillus*) or other seemingly harmless species the imaginary assailant: harmless meaning that the smaller species acted simply as a releaser and showed no sign of attack or even interest. Examples of this behavior noted for Hairy (*Dendrocopos villosus*) and Downy (*D. pubescens*) Woodpeckers were as follows:

In December 1963, while studying the roosting habits of Hairy Woodpeckers, I had occasion to follow them in the first half hour of the day. On the 13th a female dodged about behind a tree trunk in the presence of a flock of redpolls (*Acanthis flammea*) that were feeding, and when they flew overhead, she swung around with wings outstretched again. On the following day a second Hairy Woodpecker was foraging well up in an oak. When four Pine Grosbeaks (*Pinicola enucleator*) came to the roadway below, she



FIG. 1. Downy Woodpecker dodging about in play, with a chickadee acting as a releaser. The pose, with wings out, is characteristic of *D. pubescens*, as well as other species of woodpeckers, when playing under similar circumstances.

dropped almost straight downward to the limb nearest above and started dodging. On 23 December the first female preened and scratched after emerging from her roost hole at 07:24. When a flock of chickadees came near, she immediately began dodging about on the side of the trunk away from them. In an additional episode on 26 January 1964, a male twice shifted about playfully when within 5 meters and less of a flock of Pine Grosbeaks.

Essentially similar observations were made on Downy Woodpeckers. Thus at 07:15 on 2 March 1968, a male White-breasted Nuthatch (*Sitta carolinensis*) was singing his courtship song (Kilham, 1972) to his mate 3 m away when a female Downy Woodpecker came between the two and played at dodging the male. She then flew away only to return again to within 1 m

of the male nuthatch for a second bout. Neither species showed any signs of aggressiveness. On 14 July 1968, a juvenile Downy Woodpecker took playful evasive action as a chickadee alighted close by. It then flew away only to return for more dodging. At 07:00 two weeks later the same juvenile played in similar fashion when two White-breasted Nuthatches came close, and again when a chickadee came by. After this it flew away in an erratic type of flight that may also be a form of play. The mother of the juvenile had swung around a limb when close to a chickadee the week before. Although conceivable that juveniles could learn playing from their parents, I believe, from experience with hand-raised woodpeckers, that the playfulness is innate.

A second form of playfulness is the wild, erratic flight in which a woodpecker loops in, out, and around, usually among trees. This might be regarded as just a form of exercise except that it occurs most frequently in the earliest hour of the day at the same time as the dodging and may even follow it directly. A Hairy Woodpecker on 30 January 1965, for example, dodged before a chickadee, then flew off in a wild erratic flight. This type of flight could, therefore, be a form of dodging when on the wing, as if the woodpecker were being pursued by some imaginary attacker. I have seen it many times in the field for Hairy and Downy Woodpeckers, as well as for Yellow-bellied Sapsuckers (*Sphyrapicus varius*), and a few times for the Pileated (*Dryocopus pileatus*), the Red-cockaded (*Dendrocopos borealis*), Red-bellied (*Centurus carolinus*) Woodpeckers, and Common Flickers (*Colaptes auratus*).

The wild, erratic flights may be a form of play not restricted to woodpeckers. Nice (1943), for example, states that "the chief form of play which occurs in young Song Sparrows I have called 'frolicking' which . . . is characterized by runs or flights with sharp turns."

Observations on captives.—Dodging was an almost daily event soon after I turned on lights at about 05:30 in aviaries where I kept various hand-raised woodpeckers. I was thus able to note some aspects of play that I might have missed otherwise. Play might be by members of either sex. Downy Woodpeckers often started dodging on the lower side of an upright, slanting log when a sapsucker flew overhead. This behavior was only noted early after the lights were turned on, and I almost never found that the woodpeckers reacted to the sapsuckers in this manner later in the day. There was no interspecific hostility. A Downy Woodpecker usually held its wings fully extended and straight out behind its back (Fig. 1), closing them intermittently as it shifted about. The fully extended wings seemed to give Downies as well as other woodpeckers speed, agility, and balance in shifting around

one side of an upright log, then the other. It should be emphasized that the wings were never held up and outward as in a threat display. This was brought out clearly in the case of a female Pileated Woodpecker I kept for two and a half years. She was very playful at dodging and might wave her wings as well as extending them when a flicker started flying about. The Pileated Woodpecker often raised her crest as she moved her head and long neck to peer around at her fancied assailant. Later in the day a flicker might fly very close without disturbing her at all. One day, however, the Pileated looked up from the log where she was working to find a Red-bellied Woodpecker in an aggressive pose just above her (Kilham, 1961). She immediately went into a threat display, wings held out horizontally and somewhat back, rapping on the log as she did so (Kilham, 1959a). This was a "serious" response to a really aggressive threat, and distinct from dodging. When the Red-bellied Woodpecker left, she resumed feeding peacefully. The Pileated Woodpecker, in spite of its comparatively large size, sometimes flew about the aviary in wild, erratic flights. These were always taken within a short interval after leaving the roost hole, when there was no sign of her being disturbed.

Several Hairy Woodpeckers that I raised in New Hampshire were kept in an aviary with Red-breasted Nuthatches (*Sitta canadensis*) and other birds. Although the Hairies never played the dodge game with each other or with Downy Woodpeckers, they did so frequently with the nuthatches, following their every movement as they flew about, sometimes for as long as 3 or 4 minutes.

Early in the year I had placed the Hairy Woodpeckers in a large glass-sided cage, soon after they had passed from the nestling stage. Here one juvenile, a few mornings later, dodged about on an upright stick before a house fly buzzing against the glass. Thus, as on previous occasions, small imaginary assailants appeared to be the best releasers.

My Yellow-bellied Sapsuckers also played at dodging but did this at times with other sapsuckers. They were the only woodpeckers to dodge before their own species. A possible explanation is that juvenile sapsuckers, as observed in the wild, stay together in family groups (Kilham, 1962) and are comparatively tolerant and playful with each other. I never observed dodging among captive flickers. This may be because they are ground feeders and hence less adapted to shifting about on upright logs and tree trunks.

PLAY VERSIONS OF COURTSHIP IN IMMATURE WOODPECKERS

While my flickers and Red-bellied Woodpeckers did not carry on the erratic flights and dodgings of the other captive woodpeckers, they appeared to have the same exuberant sense of play, manifested in other ways. Flickers,

for example, perform bill-waving dances as adults (Kilham, 1959b). These are accompanied by "chewki, chewki" notes both in courtship and in performance of the dances against rivals of the same sex. My hand-raised juveniles began performing these dances to each other within three weeks of the time they would have fledged and it soon became a daily event that I interpreted as play. Many of these dances, as seen among wild flickers in autumn months, might conceivably be interpreted in the same way if the birds were immatures as I knew my captives to be.

The Red-bellied Woodpeckers had several activities that appeared to be play. As described elsewhere (Kilham, 1958, 1961), this species does much tapping, beginning in midwinter. One of my hand-raised females that was unusually tame did a great deal of tapping on various objects about the aviary beginning in September of her first year, when she was three months old, both to me when I entered the room and to a Pileated Woodpecker in the same cage. The tapping of Red-bellied Woodpeckers may thus be like the dances of flickers, an integral part of the courtship of adults but performed as play by juveniles at an early age.

PLAY VERSION OF FOOD STORING

The Red-bellied Woodpeckers had an additional form of play of a different nature. This as mentioned previously (Kilham, 1963), consisted of storing "miscellaneous objects of no apparent value. When I gave one female a bent, 3-inch nail, she spent five minutes trying to insert it into various holes, hunching her shoulders forward as she did so. Toothpicks, clips, or even small wads of paper elicited similar behavior. The woodpeckers would also store objects of their own, particularly a male, which would sometimes loosen a sliver of wood several inches long, arrange it to point straight forward in his bill, then fly about the aviary in search of a storage place. This same male was preparing to store another and smaller chip on 6 April, when his mate flew up, took the chip in her bill, and flew off with it." Storage of miscellaneous objects was limited to *C. carolinus* with one exception. This was on a single occasion when a Yellow-bellied Sapsucker tried to store a chip of wood in six different holes before finding one that was suitable. Eibl-Eibesfeldt (1970) describes a not dissimilar handling of sticks in play by young Woodpecker Finches (*Cactospiza pallida*).

Storage of odd objects has also been described for Acorn Woodpeckers (*Melanerpes formicivorus*). Ritter (1921) gave his opinion of the habit in this species by stating that "the [storing] instinct sometimes goes wrong to the extent of storing pebbles instead of acorns, thus defeating entirely the purpose of the instinct." It is not always easy, however, to perceive the purpose of what animals are doing. "Play," for example, may not be a case

of "instincts" gone wrong so much as a way of developing and practicing skills against a time when an animal may need them for survival. Play, according to Eibl-Eibesfeldt (1970), is learning.

DISCUSSION

Thomson's *Dictionary of Birds* (1964) states of play that it is "a form of activity much less apparent than in many mammals, but nevertheless occurring and not exclusively in the young," although few examples, it continues, are known among adult birds. Thorpe (1956), however, states it as evident that true play is fairly widespread among birds and gives numbers of references to play among ravens, hawks, hornbills, and other groups. So far I have encountered no references to play in the Picidae. Play among woodpeckers as described above is essentially no different in some of its forms from that described for other groups.

Hand-raised woodpeckers were a special asset to the present study of play for several reasons. One was that by turning on aviary lights at 05:30 I had an opportunity to see a number of species in the half hour or less after roosting, which is the time of day when they are most exuberant and playful. A second asset was tameness. Not all of my captives were tame, for some of them became quite wild in spite of my having taken them from the nest at an early age. It was the ones that were the most tame and not disturbed by my presence that were the most playful. This suggested that even if a woodpecker is not disturbed enough to fly away in the presence of an observer in the field, he may be wary enough not to play while being watched. This may account in part for the paucity of accounts of play among wild birds. A third reason that captives offer unusually good opportunities for observing play behavior is embodied in a further remark by Marler and Hamilton (1967) that "animals play when they have nothing else to do." My woodpeckers, being provided with food, shelter, and an absence of predators, did appear to have more time for idling than they would have had in the wild.

Among definitions of play given by others, none has fitted my impressions better than that of Armstrong (1947). According to him, "Surplus vitality may manifest itself in many ways which are commonly described as playful when, apart from the exercise involved, and their function in providing a means of expression for exuberant energy, they do not directly serve some biological end." The idea of "surplus vitality" is one that I have found particularly applicable. Armstrong goes on to add that play may "acquire value, as, for instance, when playful combats . . . serve as training for serious fighting in later life." He might have added "for escape from predators" as well as for serious fighting.

Hairy and Downy Woodpeckers swing under limbs and dodge behind

trunks when in actual combat. Being more or less solitary as adults, or at least not as gregarious as flickers, they do not usually play with each other as juveniles or as young adults, possibly because the mock combat of dodging might be interpreted as threat or fight evoking. This may explain why they seek out harmless species as chickadees that give them something living to dodge away from.

A final conclusion is that play among birds is a subject worthy of more attention than it has received. If play is left out of one's studies, it is possible that something of vital importance has been omitted in the understanding not only of the ontogeny of social and other behavior, but also of the total way of life of the species concerned.

SUMMARY

In observations made in the course of 16 years in the field and in eight years for captive individuals, a number of forms of behavior appeared to serve no immediate function and, in their lack of "seriousness," were clearly recognizable as play. As with other animals, the play was a version of some major pattern of behavior and these, in this report, included agonistic, courtship, and food-storing.

Play versions of agonistic (or defensive) behavior were of two types: (a) a form of play in which a woodpecker dodged about a tree trunk, with wings extended straight out backward before a chickadee or other small bird used as an imaginary assailant. Dodging was observed for Hairy and Downy Woodpeckers in the field and for these two species as well as for Yellow-bellied Sapsuckers and a Pileated Woodpecker in captivity; (b) a wild, erratic type of flight which was seen in a total of seven species, and in four of them in the aviary as well as in the field. These flights sometimes followed the dodging.

Play versions of courtship were noted for immature captives of both Common Flickers and Red-bellied Woodpeckers, when only a few months of age. For the flickers, this play consisted of bill-waving dances performed among pairs of juveniles and for the Red-bellied Woodpeckers in miscellaneous tapping performed on slight provocation.

The Red-bellied Woodpeckers, in what was interpreted as a play version of food-storing, picked up miscellaneous objects, such as bent nails, and tried to store them in crevices. This type of play was also observed once in a Yellow-bellied Sapsucker.

All of the woodpeckers were most exuberant and playful in the first half hour of the day after roosting. Only those individuals, however, that were the most tame and the least disturbed by the observer made good subjects for the study of play.

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RAPTOR TELEMETRY RESEARCH SURVEY REPORT

The Bio-Telemetry Committee of the Raptor Research Foundation, Inc. has recently completed this 47 page report, compiled by Mark R. Fuller, Thomas H. Nicholls, and Thomas C. Dunstan. It consists of detailed comments and techniques from about 40 people who are using or thinking of using radio transmitters to study raptorial birds. A list of publications dealing with raptor telemetry and a list of commercial suppliers from which telemetry equipment can be purchased are also included in the report. The report is available for the price of \$1.00 by writing: Raptor Research Foundation, Bio-Telemetry Committee, c/o Biology Department, University of South Dakota, Vermillion, SD 57069, USA.

OBSERVATIONS ON THE HORNED SCREAMER

FRANK B. GILL, F. J. STOKES, AND C. C. STOKES

Very little has been reported on the habits and behavior of screamers, aberrant anseriformes in the family Anhimidae. The Crested Screamer, *Chauna torquata*, is perhaps the best known, based on the descriptions of Hudson (1920) and Wetmore (1926). The other two species in the family, *C. chavaria* and *Anhima cornuta*, are known primarily from observations of zoo birds (Lint, 1956; Bell *et al.*, 1970). During a recent visit to Colombia, South America, we were able to study briefly the behavior of the Horned Screamer, *A. cornuta*.

The study area at Lake Mozambique was 70 kilometers east of Villavicencio in Meta Province, on the western edge of the llanos. The lake achieves a maximum width of about 2 kilometers in the wet season, from April to December, when the water level rises three meters or more. Our stay at Lake Mozambique extended from 19 to 28 February 1970. This corresponded with the latter part of the dry season, with the lake near its lowest level and the green growth of the exposed shores still young and tender.

GENERAL HABITS AND NUMBERS OF SCREAMERS

All the Horned Screamers were concentrated along the borders of the lake. During the early morning they perched conspicuously on tops of trees and large bushes near the lake edge, where they were easily observed from our boat on the lake. Our observations began at dawn and continued for about three hours, until the birds dropped to the ground and usually out of sight, to feed. We also made a few observations at midday and in late afternoon.

The Horned Screamers that we observed were usually in pairs, but single birds were also seen. These singles would frequently join a pair, and a pair would sometimes join another pair. The largest group of individuals together that we saw was six birds. Individual groups were rarely spaced closer than 25 m and were usually 100 m or more apart. Of the total population of 35 screamers on the lake, approximately 26 were stationed as groups along the southwestern border of the lake. The rest were isolated groups of one to four birds stationed at about one-half mile intervals along the lake edge. These groups kept to themselves and at no time appeared to intermingle. The entire population of this general area seemed to be concentrated at the lake.

During our observations the birds were usually sedentary. Individuals remained on a single perch for as much as two hours during the early morning, prior to feeding, and even when feeding they tended to remain within 100 meters of their perches. The relocations that did occur rarely involved flights of more than 200 m. During the eight mornings of observing screamers on the southwestern lake shore, we saw only three or four flights of as

much as 400 m. One bird was seen flying across the lake, a distance of approximately 1000 m. To our surprise, it steadily lost altitude when half-way across, bounced off the surface of the lake 100 m from shore, and skimmed to a perch only two meters high.

No birds were seen soaring during our ten-day stay, although by 09:00 each day cumulus clouds had formed and on many occasions Wood Storks (*Mycteria americana*) were soaring. Henry Mirick, H. R. Roberts, and the resident manager, A. Fisher, never saw soaring during observations of screamers that covered three years at the lake (pers. comm.). This differs from *C. torquata* which frequently soars for hours, even on windless days, and attains great heights (Hudson, 1920; Wetmore, 1926; Gill, pers. obs.).

The screamers were not nesting at the time of our visit in February, but W. J. Smith (pers. comm.) found three nests with eggs in August 1969, and H. R. Roberts (pers. comm.) photographed a nest with three eggs on 2 December 1971. The nest found by Roberts was a mat approximately one meter in diameter comprised of dried marsh grasses. The nest was 8–10 cm deep and was just floating in about 8 cm of water.

VOCALIZATIONS

We were able to distinguish three basic vocalizations (Fig. 1).

Moo Co—a bisyllabic call in which the second syllable was distinctly lower in frequency than the first. The quality of this call varied from fairly pure melodic notes to harsh barking or coughing notes. Such variation may, in part, have reflected sexual differences (see below). The intensity of *Moo Cos* also varied from soft vocalizations that can be heard only when close to the bird to loud calling that can be heard up to a mile away. On some occasions the first syllable was given without the second. *Moo Cos* were usually repeated at 3–10 second intervals.

Isolated pairs of screamers often gave *Moo Cos* together in a duetting sequence. The result was a trisyllabic vocalization, *Ha Moo Co*, or sometimes, *Ha Moo-o Co*. Such duets consist simply of an overlap of one bird's second note with the other bird's first note. To our knowledge the trisyllabic vocalization was never given by a single screamer. This calling is responsible for the screamers' local name, *jamuco*.

Lint (in litt.) observed a single breeding pair of these screamers at the San Diego Zoo and found that the male's voice was louder and deeper pitched ("baritone to tenor") than the female's ("alto to contralto"). We were able to distinguish similar vocal differences between members of a pair that gave *Ha Moo Co* duets at our close approach. The second voice was lower pitched and harsher, almost a barking, than the other. Lint's observations lead us to believe that this was the male.

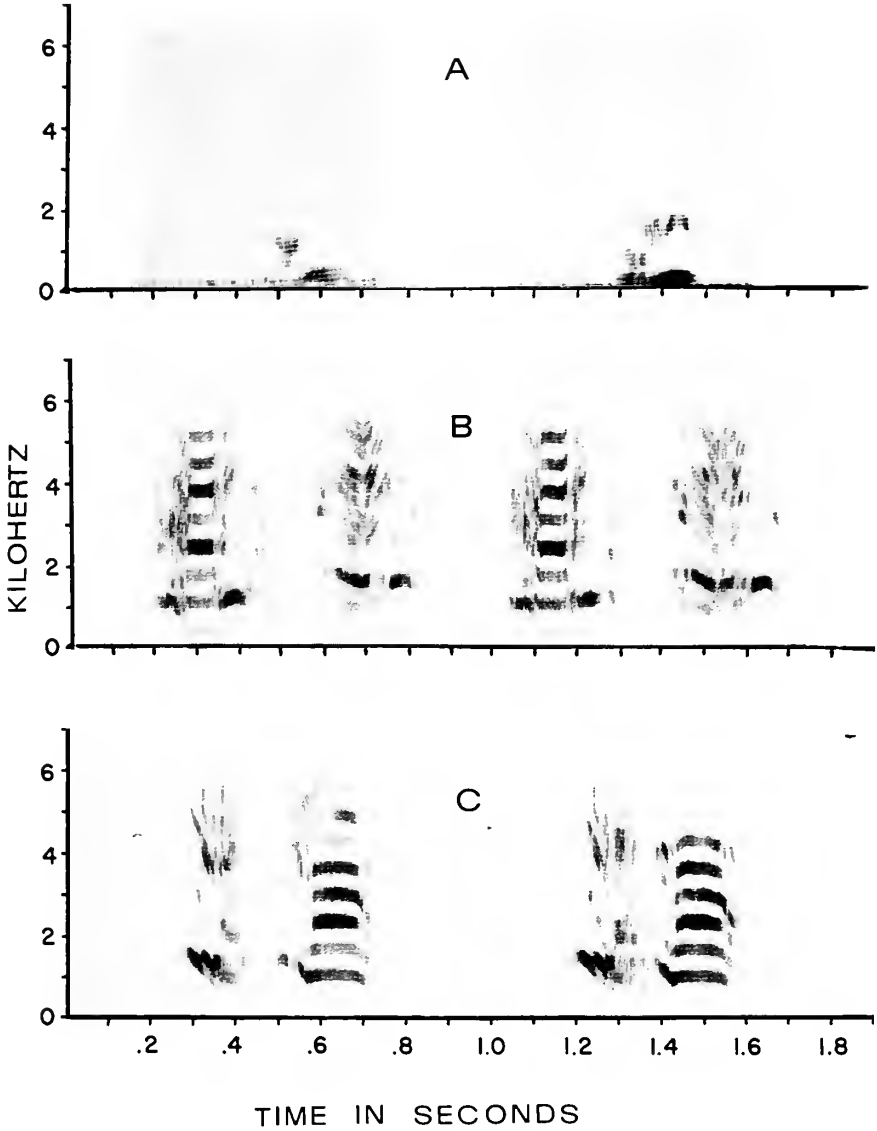


FIG. 1. Horned Screamer Vocalizations. A. Moo Co; B. Honking; C. Trumpets.

Honking—goose-like calls of two distinct patterns, given in various combinations including in alternation. One of the two patterns had seven to eight strongly developed harmonics spaced at intervals of about 750 Hz above a fundamental frequency of about 450 Hz (Fig. 1). The dominant frequency

(darkest harmonic on the spectrogram) was at 2600 Hz. The first, third, and fifth harmonics were all more amplified than the others. The other pattern, which sounded lower, consisted of a dominant frequency at 1800 Hz with only weakly developed harmonics. A typical Honking sequence lasted about 30 seconds and was often accompanied by regular bobbing of the head and neck, especially when two screamers were together. Moo Cos and Trumpets (see below) were sometimes inserted into a Honking Sequence.

Trumpet—a loud bugle-like call that carried more effectively over long distances than the other calls. It consisted of a low diffuse introductory note followed by an inflected note with a fundamental frequency at 1000 Hz and four to five well-developed harmonics. The dominant frequency was at 2600 Hz, as in the one Honking pattern.

On one occasion we watched for several hours a lone screamer perched in a tall tree by the edge of the lake. This individual called regularly, partly in response to calls from the other side of the lake. A calling sequence usually began with a series of Moo Cos that increased in intensity and then shifted into loud Honking. The Honking consisted of both notes in various combinations and, on some occasions, included interspersed Moo Cos and Trumpets. Even in more complex situations, with two or more individuals Honking, sequences were usually preceded by a short series of Moo Cos of increasing intensity. Trumpetings were nearly always associated with Honking.

Soft Moo Cos were the first screamer vocalizations heard in the early morning. Typically calling was initiated twenty minutes before sunrise and continued for only about five minutes. Vigorous calling, including Moo Cos, Honking, and Trumpeting, began at sunrise from around the lake and continued sporadically until about 09:00, when the birds began feeding. Only occasional calls were heard during the rest of the day. At sunset some pairs called briefly just after flying up to the elevated perches that may have been their roosts, but we heard no conspicuous evening chorus.

Movement of individuals between perches in trees was often accompanied by some calling. Only three of 30 lone individuals called before taking off, but if several birds were present at the departure, Honking occurred about 30 percent (10 of 33 cases) of the time. Typically (32 of 44 cases), the moving individual was greeted with Honking by others as it approached them, and after it landed all individuals Honked loudly for one to two minutes. A lone individual landing on an unoccupied perch rarely called (only three of 19 cases) and flying birds never called. The calling that accompanied these relocations stimulated calling by adjacent groups of screamers 76 percent of the time. Movements from trees to the ground were usually accomplished silently, except for occasional calls by adjacent groups.

Bouts of calling between isolated groups, up to one mile apart, were a conspicuous component of screamer vocal activity. Typically such calling involved extended Honking sequences with some Trumpeting. Particular groups or individuals seemed to respond to the calling of another group approximately 15 seconds after the calling was heard. Sequential calling between isolated groups lasted up to 20 minutes, but usually was not more than ten minutes, with individual groups calling at approximately one minute intervals. A maximum of five of the seven isolated groups were involved in any one bout. No consistent pattern of sequencing between groups could be discerned.

Some evidence of responsiveness to vocalizations was obtained by W. E. Lanyon (pers. comm.) during his visit to Mozambique in May 1972. He recorded a pair that was Honking and Trumpeting several hundred yards away and played the recording back to them. The pair of screamers promptly flew to the trees overhead and gave repeated Moo Cos, Ha Moo Cos and occasional Honking.

In general, Moo Cos tended to indicate alarm or disturbance by potential predators or the relocations of other screamers, but were also included in distance calling and greeting. Honking was used in both greeting and in distance calling. Trumpets were used primarily in distance calling but occasionally in high intensity greeting.

DISCUSSION

Outside of pairs or family groups, Horned Screamers appear to be only semi-social in their habits as we saw no conspicuous flocking. Such pairs or family units associated loosely in a remote corner of the lake where good grazing existed. We could not tell if the members of this association were mainly subadult birds, though with more experience or at closer range this might be discernible on the basis of the length of the horn (Spence, 1959). Pairs scattered around the lake may have been established adults. Distance communication between such pairs seemed an important routine.

In most respects, Horned Screamers seem to resemble the Crested Screamer, *Chauna torquata*. The latter typically occurs in pairs (Wetmore, 1926; Hudson, 1920), but unlike the Horned Screamer, it may sometimes occur in large grazing flocks of a thousand or more birds (Hudson, 1920). The nests are similar but Horned Screamer eggs are olive-brown rather than white as in the Crested Screamer. Like the Crested Screamer (Stonor, 1939), male Horned Screamers share in the building of the nest and incubation (Lint, 1956). Horned Screamers appear to have a poorer flight capacity than

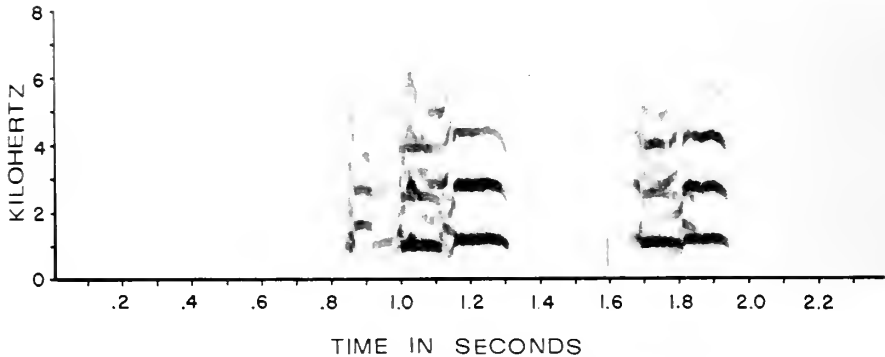


FIG. 2. Typical "chaja" Call of the Crested Screamer, *Chauna torquata*.

Crested Screamers, judging from their relatively few and short flights and the absence of soaring.

The common double-noted trumpeting call of the Crested Screamer (Fig. 2), is similar in structure to the Trumpet Call of the Horned Screamer though it contains fewer harmonics. Hudson (1920) indicates that a similar call may function as an alarm cry in the Crested Screamer, but does not describe any Moo Co-like call. Crested Screamers also have a loud singing ceremony involving both the male and female, or sometimes a whole flock (Hudson, 1920:133). This is probably homologous to what we have called Honking. Male and female *Chauna* do not have different calls (Kear, 1970: Lint. in litt.).

The fundamental frequencies of Horned Screamer sounds are low and similar to those of Magpie Geese (*Anseranas semipalmata*) and large swans (Johnsgard, 1972), in which long-distance communication is also important. If the trachea of Horned Screamers is acting as an open tube system, as appears to be the case in other waterfowl, such sound production suggests a tracheal length of about 30 cm, which is as long as that of a large swan. However, we have not found any published description of a screamer trachea.

Screamers have traditionally been allied with the Anseriformes (Johnsgard, 1965; Kear, 1970; Sibley and Ahlquist, 1972). In particular, screamers resemble the Magpie Goose in behavior, that of the latter containing many primitive features (Johnsgard, 1965; Kear, 1970). Sexual dimorphism in voice, found in the Magpie Goose (Johnsgard, 1972) and the Horned Screamer—but not in *Chauna*, is lacking in the Anserinae but is present in more advanced ducks. The Magpie Goose has well-developed preflight signals including lateral headshaking and associated goose-like calling (Johnsgard, 1965). Such behavior seems lacking in the Horned Screamer, which calls

irregularly and to our knowledge did not shake its head before taking off. Low intensity threat displays and triumph ceremonies involve wing shaking in the Magpie Goose (Johnsgard, 1965), versus shelduck-like wing flapping in the Horned Screamer (Spence, 1959). It seems likely, therefore, that the resemblances between screamers and the Magpie Goose could be only superficial and convergent (Davies and Frith, 1964).

SUMMARY

A population of 35 Horned Screamers was observed for eight days in the llanos of Colombia. The birds tended to be sedentary, remaining on a single perch for as much as two hours during the morning. Occasional flights to new perches were rarely longer than 200 m. The birds were never seen soaring and only rarely seen flying.

Three basic vocalizations were used—loud goose-like Honking and Trumpeting and a somewhat melodious Moo Co. Calls were limited almost completely to the morning hours before the birds fed. Isolated pairs frequently duet with the Moo Co. primarily in response to disturbance. Arrivals of relocating individuals were typically accompanied by Honking, often with head bobbing. Communication between groups scattered around the lake involved Honking, Trumpeting and Moo Cos. The low fundamental frequencies and the well-developed harmonic of these calls suggest a long trachea (about 30 cm).

Comparison is made with the other two members of the family—*Chauna chavaria* and *C. torquata*, and the behavior of certain waterfowl, especially the Magpie Goose, *Anseranas*.

ACKNOWLEDGMENTS

We are particularly grateful to Mr. and Mrs. W. B. Dixon Stroud who made possible our visit to their ranch at Mozambique, and also to Mr. and Mrs. Alexander Fisher, for their generous hospitality. W. E. Lanyon made available his field observations and recordings of *Anhima cornuta* and *Chauna torquata*. We are also grateful to H. R. Roberts, Henry D. Mirick, and W. John Smith for their observations from Mozambique and to P. Johnsgard for critical comments.

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NOTES TO AUTHORS IN THE WILSON BULLETIN

Currently, the Wilson Bulletin is enjoying lead times of as little as four to six months on papers received in good condition and that receive prompt attention from referees. We would like to keep lead times short, but we do foresee some buildup of manuscripts in print and awaiting publication. Consequently, authors may read proof on articles that will not appear in the next issue, and this notice will forewarn you of that possibility.

As a change in editorial policy, all authors are asked to specify if they wish illustrative materials (other than color plates) returned to them after printing. The policy, starting with this issue, will be *not* to return such material unless specifically asked to do so. In many cases, illustrations may be discarded by authors after printing, and we can save postage by doing this without returning them to authors. We will keep illustrations in our files for one year before disposal, but we urge that authors request return as soon as possible—preferably when papers are submitted.

Finally, we ask authors to be apprised of the cost of changes once an article is in galley proof. The Bulletin is billed at 75 cents per line changed, except when due to printer's error. Note that even a simple change calls for an entire line to be redone. If a change is longer than the space available in a line, it may well require that following lines in a paragraph also be changed. Thus, a minor change at the beginning of a paragraph may result in the whole paragraph being reset, at 75 cents per line. In the past, authors have been allowed a few changes without charge; however, to economize we now expect to charge for every line altered due to author's error or change.

OBSERVATIONS AT A CAROLINA WREN NEST FROM WHICH BROWN-HEADED COWBIRDS FLEDGED

DOROTHY HOBSON LUTHER

Records of Carolina Wrens (*Thryothorus ludovicianus*) fledging Brown-headed Cowbirds (*Molothrus ater*) are rare, with only one instance reported among a dozen or so known parasitized nests (Friedmann, 1963:39). Most of the evidence that this species successfully hosts cowbirds is circumstantial and includes infrequent reports of fledgling cowbirds being fed by wrens. In view of this lack of data, I present my detailed observations of a banded pair of these wrens, which successfully fledged three cowbirds. The observations were made at our 12-acre bird sanctuary near the Pine Hills Nature Preserve, Shades State Park, in Montgomery County, Indiana. I spent about 35 hours at the task, observing without a blind 18 feet from the nest.

The wrens' nest was in a shallow, cardboard fruit basket (12 × 8 × 4 inches), suspended six feet above ground beneath the broad eaves of a flat-roofed building. The previous year I banded the wrens as young of the year, the female on 22 May, the male on 9 September. In 1972 I retrapped them and added color bands, later sexing them by their behavior. On 7 June these inexperienced wrens completed their nest, leaving an unusually large opening above the rim of the basket, which faced outward in full view, a boon to the cowbirds and to me as well.

Between 7 and 17 June four Carolina Wren eggs and three Brown-headed Cowbird eggs were laid in the nest, but a wren egg was probably removed by a cowbird. Two cowbirds evidently deposited the eggs because two eggs of this species were laid in the nest on the same morning. On 18 June and again on 21 June, single wren eggs vanished, leaving three cowbird eggs and only two wren eggs.

The cowbird eggs hatched on 22 and 23 June, while those of the wrens did not hatch until 26 and 27 June. The last-hatched wren died soon after hatching, apparently crushed by the weight of the three much larger cowbirds. On the next day the other wren was gone, presumably having died and been removed by its parent.

FEEDING OF YOUNG

During 29 hours of observation, I obtained data on the hourly rate the pair of Carolina Wrens fed the three cowbirds. Unfortunately, I could not be at the nest, except for brief periods, until the cowbirds were four and five days old. Therefore, the following data are based on observations made

TABLE 1
NUMBER AND RATE OF FEEDINGS OF NESTLING COWBIRDS BY WRENS

| Date 1972 | Hours watched | Feedings | | | | | | Remarks |
|--------------|------------------|---------------|------|---------------|-------------------------------|---------------|----------------|--|
| | | Total per day | | | Average per hour ¹ | | | |
| | | by ♂ | by ♀ | by ♂ and ♀ | by ♂ | by ♀ | by ♂ and ♀ | |
| 27 June | 9 | 37 | 29 | 66 | 4.1 | 3.2 | 7.3 | 3 cowbirds (ages 4 and 5 days), 2 wrens (ages 0 and 1 days); 1 wren dead by 16:15. |
| 28 June | 1 | 11 | 3 | 14 | 11.0 | 3.0 | 14.0 | 3 cowbirds, last young wren gone by early morning. |
| 1 July | 3 | 29 | 26 | 55 | 9.7 | 8.6 | 18.3 | 3 cowbirds. |
| 2 July | 5 | 63 | 39 | 102 | 12.6 | 7.8 | 20.4 | 3 cowbirds. |
| 3 July | 11 | 115 | 129 | 244 | 10.5 | 11.7 | 22.2 | Cowbirds (ages 10 and 11 days) fledged at 07:04, 19:46, and 19:53. |
| Totals | 29 | 255 | 226 | 481 | \bar{x} 8.8 | \bar{x} 7.8 | \bar{x} 16.6 | |

¹ Determined by dividing total feedings by number of hours watched.

on five of the last seven days the cowbirds were in the nest (which included the single day the two wren nestlings were present).

The wrens brought 481 meals during this period, the female carrying 226 of these and the male 255. The average number of feedings per hour was 16.6, 7.8 by the female and 8.8 by the male. Food appeared to be largely composed of spiders of various sizes, including harvestmen or "daddy long-legs," and occasional caterpillars and moths. Only one young was fed per trip. A summary of the number and rate of feedings is given in Table 1.

On 27 June I observed the nest for a nine-hour period and found the feeding rate to be only 7.3 times per hour. This low rate apparently was the result of the very large size of insects consistently brought to the young, insects too large even for the cowbirds to swallow easily. In one instance the male made nine attempts before successfully feeding a large spider to a cowbird. This was the one day on which the complete brood of three cowbirds (four and five days old) and two wrens (one a day old and one hatched that morning) was present. On the following day, after the two young wrens had died, the parents consistently brought small insects, and the feeding rate doubled.

Apparently the parents treated the mixed brood of five as a normal one in which there were weaklings: in this case the weaklings were their own nestlings. Neither parent fed the young wrens while I watched during the nine hours on 27 June. The older young was too weak to compete for food, whereas the wren hatched that morning was never able to get out from under the much larger cowbirds, which completely covered and trampled it.

On 3 July, fledging day, the foster parents brought 244 meals during my 11 hours of observations, the female carrying 129 of these and the male parent 115. In the first hour, the wren pair fed the three young cowbirds 28 meals at the average rate of 9.3 per nestling. The female fed 15 meals and the male 13. At the end of that hour, the first cowbird fledged. With two cowbirds remaining in the nest, the rate peaked in the following hour at an all-time high of 39 meals (20 of these were brought by the female and 19 by the male), with the rate of 19.5 meals per nestling per hour. By comparison, the average hourly rate of feeding on that day was 22.2. Since the fledged cowbird was not visible to me, I could not see how frequently it was fed.

Nice and Thomas (1948:157), observing at an unparasitized Carolina Wren nest, found the rate of feeding during the hour immediately prior to the fledging of a brood of five was 18 meals per hour (7 by the male and 11 by the female). Had the wrens fed equally, each would have received 3.6 meals. During that hour on fledging day in my study, the foster parents fed a total of 10 more meals per hour to three cowbirds than the wren parents fed to Nice' and Thomas's five wren nestlings. These figures indicate that if the individuals were fed equally within each nest, each cowbird would have received 5.7 more meals during that hour than did each wren. The parasites were age 10 and 11 days, the wrens 13 and 14.

When the young in each nest were five and six, eight and nine, and nine and ten days old, respectively, I found that "my" wrens averaged 17.6 feedings per hour per day, while those studied by Nice and Thomas averaged 11.2. Thus, the cowbirds received an average of 6.4 more meals per hour daily than did the wrens. Individual cowbirds, therefore, were fed at the rate of 5.9 meals per hour per day, the wrens 2.2 during these three days.

Laskey (1948:109) found that when two Carolina Wren nestlings were 10 days old, the average number of meals brought per hour was 6.1, compared to 21.6 the two remaining cowbirds of my study received at the same age. Therefore, the cowbirds were fed 15.5 more times per hour than were the wrens. This was at the hourly rate of 10.3 meals per cowbird, versus 3.0 meals per wren. Thus the cowbirds were fed over three times as frequently as were the wrens. Laskey observed for 7.4 hours and I observed for 10

during this period of comparison. (Her overall study is based on 81.1 hours of observation.)

The above comparisons suggest an increase in the feeding rate by Carolina Wrens when they are parasitized. The greatest degree of difference, 15.5 more meals per hour for the cowbirds, occurred in comparing the feeding rate when only two 10-day old young were in each nest. This was on fledging day for the cowbirds and three days short of that day for Laskey's wrens. Comparison with Nice and Thomas indicates that "my" wrens made from six to ten more trips per hour per day to feed three cowbirds than they would have with a normal brood of five wrens. However, the wren nestlings fledged at 13 and 14 days, while the cowbirds of this study departed at 10 and 11 days.

DISPOSAL OF FECES

During my observation, fecal matter was carried from the nest 35 times by the male wren and 13 times by the female: it was swallowed on 12 occasions by the male and on 3 by the female. After the cowbirds were eight and nine days old, removal of excreta, no longer encased in mucal sacs, appeared to be difficult when the long stringy mass frequently broke. On the last day in the nest, the young occasionally backed to the rim to defecate. Laskey (op. cit.) reported some fecal sacs were swallowed by the parents in the early days of nest life, but Nice and Thomas (op. cit.) apparently did not observe this behavior.

DEFENSE OF THE NEST

The female wren appeared to take no part in defending the nest: her mate did little more than *chirr* at possible predators, except chipmunks (*Tamias striatus*). When a chipmunk peered into the nest, the male wren flew at the rodent, pecked it, and chased it away. A House Wren (*Troglodytes aedon*), nesting nearby, pursued a chipmunk until it ran through a length of pipe to escape, but as the animal scurried out a few seconds later, the male Carolina Wren immediately took over the pursuit. Fox squirrels (*Sciurus niger*) were completely ignored, but the male wren *chirred* at a cottontail rabbit (*Sylvilagus floridanus*) that was sitting on the roof placidly eating leaves of an overhanging limb. (The building against which the nest basket was suspended abuts against a hill.) The Carolina Wrens were not present when a two-foot-long milk snake (*Lampropeltis dolia*) on the roof dangled its head to within a foot and a half of the nest. The serpent probably was not very hungry: judging from the lumps in its body, I suspected the snake had been feeding on frogs that frequent the roof. Six hours later when the same snake attempted to attain the nest from the ground, the male wren sang loudly.

LEAVING THE NEST

On 3 July I watched the wrens' nest almost continuously from 06:00 until the three cowbirds, now banded, had departed. At 07:04 the female wren flew from the nest after feeding the oldest nestling, bird 1. Apparently triggered by her flight, the cowbird, age 11 days, left the nest, landing in vegetation about five feet away. There it remained for almost an hour. At the end of the second hour, it had progressed about 10 feet by fluttering on or near the ground.

Bird 2, age 10 days, departed at 19:46, after having been fed at 19:00 by the male wren which sang loudly from the roof as if encouraging the young to leave. Bird 2 flew from the rim of the basket to a sapling about five feet away, then fluttered to a lower limb.

The remaining cowbird, bird 3, age 10 days, left the nest at 19:53, almost 13 hours after bird 1 had flown. The female wren was also in the bottom of the basket when this cowbird suddenly flew up toward the roof overhang, then fell to the ground with a slight thud, landing directly under the nest.

On the following morning I found bird 2 still in the sapling, while bird 3 had moved from the ground to a limb about two feet up and five feet from where it had fallen. I failed to find bird 1: I suspect raccoons (*Procyon lotor*) captured it.

By 10:00 bird 3 had moved up the hill about 10 feet from the nest and to within 10 feet of bird 2 now in a small tree. Their flight ability still poorly developed, the young remained in the same area all morning. These young frequently gave a location call, *seeee-eee*. The male wren sang and *chirred*: his mate occasionally uttered a tinkling call. Thus the individuals kept in touch with each other and the fledglings were frequently fed. By evening the young, encouraged by the foster parents, had moved perhaps 20 feet across the hillside toward a brook in a secluded area. I did not see the cowbirds again but the wren pair returned to the nest area eight days later.

DISCUSSION

Two notable departures from normal Carolina Wren behavior were observed. At this parasitized nest the female ceased to incubate at least 24 hours before her own last egg hatched. Apparently, the warmth from the cowbird nestlings was sufficient to hatch the remaining wren egg. Also, the female did not brood the cowbirds after the two younger ones were two days old and did not brood her last hatched wren at all. In my experience, and that of others, the female Carolina Wren typically broods her young for at least four days. The above variations were apparently aggravated by the four- and five-day headstarts of the large cowbird nestlings over the small wrens.

Why was this pair of wrens heavily victimized when Carolina Wrens are apparently rare hosts to cowbirds? A combination of factors may have been involved:

Size of cowbird population.—The cowbird population at our sanctuary has been consistently fairly large. The previous year I color-banded 24 new individuals and had 13 returns from other years, a total of 37 individual cowbirds. In the spring and summer of 1972, I made no attempt to band birds, but I did, more or less, record the color-banded returns. Eleven color-banded cowbirds were frequently observed at the feeders: five females and six males, along with a number of unbanded individuals.

Lack of nests of normal hosts.—In past years cowbirds have deposited eggs in a number of nests in our yard there, parasitizing the Red-eyed Vireo (*Vireo olivaceus*), White-eyed Vireo (*Vireo griseus*), Acadian Flycatcher (*Empidonax vireescens*), Yellow Warbler (*Dendroica aestiva*), Indigo Bunting (*Passerina cyanea*), Cardinal (*Cardinalis cardinalis*) and the Song Sparrow (*Melospiza melodia*). (One day I even saw a female cowbird looking into a hummingbirds' nest there!) However, in 1972, nests were extremely scarce in our yard, the lowest record in 20 years. I have no doubt that this paucity was the result of the havoc being wrought on the natural environment by the chain saw, bulldozer, back hoe and other activities relating to the removal of our old cabin and the erecting of our new part-time home on the site. This activity began in early spring and continued until fall. Nests in our yard that season were limited to those of the Carolina and House Wrens, the latter nesting in a wren box. This left only the Carolina Wren nest available for parasitizing. The fact that *two* cowbirds laid eggs in this nest appears to emphasize a scarcity of nests in the area.

Nest and opening too conspicuous.—Carolina Wren nests there have been, more often than not, inaccessible to cowbirds. On the contrary, the parasitized nest described here was not only conspicuously located, but also had an unusually large opening facing outward and *above* the basket rim. A bird house this species had used in past years was only six feet away but was not used. (This pair of wrens built a second nest late in the same season, after all cowbirds had left. This nest, 17 feet from the first nest and over a door of the same building, was equally conspicuously located, though the opening was smaller. Although 5 eggs were laid, only two wrens fledged on the late date of 3 September.)

Inexperience of parents.—Did inexperience of the wrens play a part in number 3 (above)? I have found nothing in the literature available to me to support a positive answer, but Pettingill (1969:343) suggests that nest-building abilities of young birds need investigation. Perhaps the following excellent nesting record was merely a matter of chance: at any rate, the

color-banded male started building a nest on the early date of 19 February 1973, this time in a secluded interior of a building. A clutch of six eggs hatched before the start of the cowbird laying season and six wrens fledged. Then a clutch of five eggs was laid in a second well-constructed nest, 15 feet from the first one and in the same building. Five wrens fledged. However, for this nest he had a new mate, his first one having disappeared. From his third nest that season, sometime between 8 and 11 September, the male and his second mate successfully fledged four young from a nest perhaps 40 feet from the first two nests of the season. I was totally unaware of this nesting until I discovered the male carrying an insect in his beak. At that time of year, tall vegetation concealed the location. This well-constructed nest is of special significance to this paper because it was located in the same basket from which the three cowbirds fledged the previous year! I assume that the old nest had been remodeled; however, the much smaller opening could not be seen above the rim of the basket and the top of the nest was barely visible. The only way I could see in *this* nest in the basket was to stand on a ladder. In his second nesting year, the male of this paper successfully raised 15 wrens as opposed to three Brown-headed Cowbirds and two Carolina Wrens his first year.

SUMMARY

A pair of first-year Carolina Wrens successfully fledged three Brown-headed Cowbirds in Montgomery County, Indiana; their own two hatchlings died within a day or two. The feeding rates in this pair of wrens was higher than those reported for non-parasitized nesting wrens—probably as a response to the demands of the cowbirds. Factors leading to this case of parasitism, which is rarely recorded in Carolina Wrens, may be related to the high local density of cowbirds, the scarcity in 1972 of normal nest-hosts, the vulnerability of the nest, and associated inexperience of the pair of wrens. Interestingly, the following year the male wren (and two new mates) built well-concealed nests and raised three broods of wrens.

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NOTES ON BIRDS OF COSTA RICA

MERCEDES S. FOSTER AND NED K. JOHNSON

These notes provide new or supplementary information on the distribution and ecology of 13 species of birds in Costa Rica. The data result from 13 months of field work by Foster, from 1966 through 1972, and 8 months of independent study in 1966 by Johnson. Common names, sequence of species, and evaluation of records are based on Slud (1964), the major recent work on Costa Rican birds. Specimens referred to are deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, where identifications were made.

LIST OF SPECIES

Double-toothed Kite. (*Harpagus bidentatus juscatus*).—This seldom seen species was taken at three widely separated localities: Alajuela Prov., 4.1 mi (= 6.5 km) NE Quesada, in scrubby second-growth adjacent to cultivated fields on 5 July 1969 (ad.; testis 12×4 mm, 186 g); Limón Prov., Estación Experimental Los Diamantes, 1 mi (= 1.6 km) E Guápiles, in second-growth woods on 26 July 1967 (ad., testis 3×1 mm, 165 g); Puntarenas Prov., Lower Sabana Esperanza, 3 mi (4.8 km) E Finca Helechales, in lower montane wet forest at the edge of a savanna on 10 September 1967 (ad., testis 5×2 mm, 172 g). One kite was captured when it attempted to catch a small bird or bat tangled in a mist net. The stomach was packed with remains of insects, primarily orthopterans.

Mirandolle's Forest Falcon. (*Micrastur mirandollei extimus*).—This rarely collected species was taken at the northern limits of the known geographic range in central Costa Rica: Alajuela Prov., 4 mi (6.4 km) NW Quesada, 1500 ft (= 450 m) on 15 May 1966. The bird (ad., ova 1 mm or less, 542 g, heavy molt, snake in stomach) was perched alone 2 m above the ground in a stand of 10–20 m second-growth riparian forest.

Barn Owl. (*Tyto alba guatemalae*).—This species probably occurs throughout the country (Slud, 1964). Foster found it extremely common in the tropical dry forested area around Estación Experimental Enrique Jiménez Nuñez (Finca Jiménez), 8.5 mi (= 13.6 km) SW Canas, Guanacaste Prov. Several to many individuals could be seen almost any evening, perched on fence posts or in trees along the dirt roads. Three specimens were collected between 7 July and 18 August 1967. The species also was observed at the Middle Sabana Esperanza, 5400 ft (= 1650 m), a locality which is considerably farther south than previous records. A female was taken there on 13 September 1967.

Striped Owl. (*Rhinoptynx clamator clamator*).—This species is proving to be rather common locally in Costa Rica. A specimen was taken by R. McDiarmid on 9 August 1967, 3.5 mi (= 5.6 km) SW Rincón, Puntarenas Prov., somewhat farther south than previously reported localities. The bird (ova to 4 mm) was perched on a power pole adjacent to an air-trip in tropical wet forest.

As reported by Orians and Paulson (1969) the species is relatively common at Finca Jiménez; there Foster took a male (testis 4 mm) and a female (ova not enlarged; very fat; grasshopper and small bird in stomach) on 11 July 1967. The female was collected from a daytime roost (07:00) in low deciduous woodland, about 2.5 m up in a small tree.

Unspotted Saw-whet Owl. (*Aegolius ridgwayi ridgwayi*).—This owl is rare throughout its range. A male (testis 8×4 mm, 84.1 g, bits of hair in stomach) was taken in large trees on the edge of a deep canyon in steeply sloping pastureland, on the south side of Volcán Irazú, 2928 m, Cartago Prov., on 16 April 1966. The bird called steadily soon after dusk on a clear and quiet evening; it was followed for approximately 700 m as it moved upslope. The rhythmic whistles seemed lower in pitch than calls of the Northern Saw-whet Owl (*A. acadicus*) and lacked the obvious oscillations in pitch and intensity that characterize that species. Marshall (1943:25) also noted the even pitch in calls of *A. ridgwayi* from El Salvador.

Common Potoo. (*Nyctibius griseus costaricensis*).—Although this species probably occurs countrywide, it has been reported from relatively few localities. According to residents of the area, it occurs regularly in the vicinity of Finca Helecheales where two were collected and a third observed at approximately 03:30 on 18 September 1967. One was perched on a 2 m fence post; the others were together on adjacent 45 to 60 cm stumps, all along a wide path through thick second growth. They perched quietly, occasionally making short flycatching sallies. The species has a bright red eyeshine in a flashlight beam.

A fourth individual, first seen by Susan Smith on 10 July 1969 at Finca Jiménez, was perched approximately 4 m above the ground at a bend in a 20 cm diameter limb of the leguminous tree, *Dalbergia retusa*. The potoo was situated at the side of the limb, with which it made a 45° angle, so that the tail was visible below the limb. The bill was held vertically and the eyes were closed. Periodic checks indicated that a potoo probably occupied the same position throughout the day on 11–14 and 18–20 July. Several attempts to eyeshine the bird at night were unsuccessful.

Because the tree was located in a relatively inaccessible tangle of thick brushy second growth, the potoo usually was observed with binoculars from a distance of approximately 25 m. On 21 July, observation at close range revealed the presence of a young bird on the bare limb, nearly covered by the breast feathers of the adult. In previously reported nestings (Goeldi, 1896; Muir and Butler, 1925), eggs were located in depressions on top of stumps where the possibility of their rolling off was slight. In this instance, there was no depression (although the bark was rough), and the limb grew at a 45° angle with the horizontal. It is difficult to see how an egg could have stayed on the limb, unless an adult were present at all times to hold it in place. The nestling clung to the limb with extreme tenacity, behavior also noted by Muir and Butler (1925).

We collected the parent and the young potoo; the former was a male (skull ossified, testis 11×8 mm, 242 g, no fat). This indicates that this sex helps in the care of the young as well as in incubation. The nestling (female, skull not ossified, ovary undeveloped, 106 g) was undergoing the postnatal molt. The juvenal plumage had completely replaced nestling down over most of the body. The primaries and rectrices had grown to approximately 15% of their adult length.

Stomach contents of both the adult and nestling were analyzed by Daniel H. Janzen. Adult beetles were the most abundant item in the stomach of the adult (Elateridae, 1; 35 mm long \times 10 mm wide; Scarabaeidae, 6; 15×8 ; Curculionidae, 1; 30×7 ; Tetti-goniidae, 1; 40×6). The young bird, which was very fat, had the stomach crammed with insect material, even though the bird was collected late in the morning (11:00). Its stomach contained adult and larval beetles (Dermestidae, 1 larva; 5 mm; Passalidae, 1; 40×10 ; Scarabaeidae, 4; 15×8 , 1; 20×10), plus approximately 15 large (10×6) chunks of hard, rotten wood. The adult insects represent nocturnally flying species and,

with the exception of the passalid, probably were picked from the air. Though passalids do fly, the presence of this one with the dermestid larva and wood suggests the material was scooped from a rotten tree trunk or limb. As there was no rotted wood in the vicinity of the young bird, we assume the adult collected and regurgitated this material. Bits of wood also have been reported in the stomach contents of *Chordeiles minor* (Rust, 1947). Interestingly, no remnants of moths were found though their scales usually persist in the gut after other parts are gone (D. H. Janzen, pers. comm.).

Pauraque. (*Nyctidromus albicollis intercedens*).—This species, common throughout Costa Rica, exhibits seasonal variation in abundance, or at least in conspicuousness, at certain localities. Pauraques were observed commonly around Finca Jiménez between 5 and 16 February. Numerous individuals called in the early evening and at dawn. The species was equally obvious in the same area between 11 and 19 August. As many as 40 individuals could be seen foraging along a 4 mi (= 6.4 km) stretch of dirt road passing through pasture and occupied in part by sleeping cattle. Usually the pauraques occurred in twos or threes. They were observed at various times between 19:00 and 22:00 but appeared most abundant between 20:00 and 21:00. During a visit to Los Diamantes Farm from 13–17 March, pauraques also were seen commonly at night along all dirt roads. A nest with eggs was located in a small clearing in open second growth vegetation on 15 March.

During visits at other times of the year to Jiménez (7–21 July; 1–2 August) and Diamantes (23–29 July), the species was rarely heard or seen. On several occasions none was detected along the stretch of road described above. The few observed were found in river bottom forest. This could indicate a seasonal shift in feeding time or locality, or result from increased secrecy during the molt period. Of five specimens collected between mid-July and mid-August, 1967, four were molting.

Cassin's Aracari. (*Selenidera spectabilis*).—Slud (1964) considered this species to be the only uncommon Costa Rican toucan. We have records of individuals observed on numerous occasions during the month of August, in and on the edge of forest and in isolated trees in clearings, 1 to 3 mi (= 1.6 to 4.8 km) south and southeast of Cariblanco, Alajuela Prov. A male (testis 10×5) and a female (largest ovum 1 mm) were collected on 5 and 15 August 1969, respectively.

Spotted Antbird. (*Hylophylax naevoides capnitis*).—Two adults were collected at Finca Jiménez on 17 May 1972 (female, largest ovum 0.5 mm) and 7 December 1972 (male, testis 2×1). This locality is only about 22 mi (= 35 km) from the northwestern divide where this antbird is reported to be abundant (Slud, 1964). However, Finca Jiménez is in an area of extremely dry tropical forest, strikingly different from the humid forests of the continental divide.

Long-tailed Tyrant. (*Colonia colonus leuconotus*).—The following records help to define the breeding season of this flycatcher in Costa Rica. This species was both abundant and conspicuous at Los Diamantes Farm from 13–17 March 1966, in low second-growth trees around cultivated clearings and in forest edge. Birds displayed commonly. Individuals would leave perches at the tips of adjacent, 3 to 4 m high branches, approach and fly vertically around each other, and return to their original places. A female collected on 16 March had enlarged yellow-orange ova up to 3 mm in diameter. Interestingly, Arbib and Loetscher (1935) found this species breeding during July and August in Panama, and Skutch (1960) located a nest in Ecuador on 30 August. During a subsequent visit to Los Diamantes and vicinity, from 23–29 July 1967, the species was rarely seen, although it was not uncommon in the forests across the Rio Toro Amarillo Bridge,

approximately 4 mi (≈ 6.4 km) west of Guápiles. This might reflect a seasonal shift in habitat use. Three birds collected at this time were not in breeding condition.

Great Kiskadee. (*Pitangus sulphuratus guatemalensis*).—The breeding season of this species apparently is greatly protracted. At Finca Jiménez, individuals were observed building nests or carrying nest material on 11 February, on 19 July (in three separate areas), and on 20 July. On 14 March at Los Diamantes, a pair occupied a nest about 15 m up in an isolated tree in scrubby second growth. A bird collected there on 25 July 1967 was also in breeding condition (testis 11×4 mm).

Olive-sided Flycatcher. (*Nuttallornis borealis*).—An early fall migrant (skull ossified, testis 4 mm, 33.9 g, light fat) was collected 25 August 1967 at Villa Mills, Puntarenas Prov.

Yellow-bellied Tyrannulet. (*Ornithion semiflavum*).—Although Slud (1964) reports a slight record of this tiny flycatcher from the Rio Frio region of northern Costa Rica, the following specimen is the first from the Caribbean slope of the country, where the very similar *O. brunneicapillum* also breeds: Alajuela Prov., 4 mi (≈ 6.4 km) NW Quesada, 1400 ft (≈ 427 m) in canopy of 25 m high riparian forest, 3 April 1966 (testis 6×4 mm, skull windows, 7.0 g). Importantly, this specimen of *O. semiflavum*, although worn, is perfectly typical of other examples of the species, from the Pacific slope of Costa Rica and farther north in Middle America. It shows no sign of intergradation with *O. brunneicapillum*, suggesting probable sympatry of the gray-capped and brown-capped forms in Caribbean Costa Rica—although specimens of both have not yet been taken at the same locality. Several recent authors (e.g., Slud, 1964; Wetmore, 1972) have assumed specific status of the two forms, presumably based on differences in coloration without known intergradation.

Olive-striped Flycatcher. (*Mionectes olivaceus olivaceus*).—This species is known from the vicinity of the Aguacate Mountains and the Cordillera de Guanacaste (Slud, 1964), but has not been reported from the Cordillera de Tilarán. On 25–26 February 1966 four individuals were netted and released at Monteverde, Puntarenas Province, and on 27 June 1967 a male was collected at El Silencio, Guanacaste Prov.

Black-and-yellow Tanager. (*Chrysothlypis chrysomelas chrysomelas*).—Two breeding adults (σ , testis 6×4 mm; ♀ , ovum 5 mm) of this uncommon tanager (Slud, 1964) were taken along a road through primary forest, approximately 1.5 mi south of Cariblanco, on 2 and 6 August 1967. These birds and individuals observed on other occasions were present in mixed species flocks which included *Chlorophanes spiza*, *Cyanerpes lucidis*, *Tangara florida*, *Chlorothraupis carmioli*, and *Cacicus uropygialis*.

Dotted Bush-Tanager. (*Chlorospingus punctulatus*).—A specimen of this species (catalog number 27865) was found in a batch of bush-tanagers borrowed for study by Johnson from the Field Museum of Natural History. It bears the notation "Costa Rica" and, incorrectly, "*Chlorospingus zeledoni*." Emmet R. Blake and Alexander Wetmore independently identified the specimen as the rare *C. punctulatus*, previously known only from central western Panama. According to the specimen tag, the collector was H. Whitely. As there is no positive record that H. Whitely ever collected in Costa Rica (E. R. Blake and A. Wetmore, in litt.) and because the species has not been noted by other workers in that country, the locality ascription is suspect. For these reasons *C. punctulatus* should be listed as hypothetical for Costa Rica.

Slaty Finch. (*Spodiornis rusticus barrilesensis*).—This species is rare throughout its range. Johnson took a male (testis 1 mm, rear skull windows, 15.4 g, no molt or fat) in adult plumage on 30 June 1966 on the south slope of Volcán Poás, 6500 ft (≈ 2000

m), 2.5 mi (= 4 km) W Varablanca, Alajuela Prov. The bird was with another male and a brownish individual (presumably a young male or female), feeding on the ground at the edge of a pasture near streamside woodland. They perched several times in low bushy growth scattered along the pasture border. Orians and Paulson (1969) and Stiles and Hespdenheide (1972) have recently reported this species from the area of Volcán Barba in the Central Highlands.

Peg-billed Finch. (*Acanthidops bairdi*).—This odd finch, previously encountered very rarely and not found by Slud (1954), occurred commonly on Volcán Irazú and Volcán Poás between March and August, 1966. On numerous occasions Johnson recorded 10 to 20 individuals per day. Series of skins, skeletons, and specimens preserved in fluid were collected. Orians and Paulson (1969) and Stiles and Hespdenheide (1972) also have reported recent records of the species from the highlands of Costa Rica. The possible connection between the dramatic increase in abundance of this species in the last decade and the eruption of Volcán Irazú in March of 1963 will be discussed elsewhere (N. K. Johnson, ms.).

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NEW LIFE MEMBER



Allan Reed Keith is now a Life Member of The Wilson Ornithological Society. He attended Amherst College, Harvard and Yale Universities, earning a BA at the first in 1959 and an MBA at the second in 1962. He works for a company of investment bankers, where he is vice president. He is a member of many nature-connected organizations, and his interests also extend to education. In ornithology his interests focus on distribution and systematics. He has published several scientific notes and papers, based on observations of birds or mammals in such diverse places as Tierra del Fuego, Africa, Fiji, and Samoa. He lives in New Vernon, New Jersey, and is married and the father of two children.

PLAN TO ATTEND THE 1974 ANNUAL MEETING

The Wilson Ornithological Society will hold its 55th Annual Meeting at The University of Michigan Biological Station on Douglas Lake near Cheboygan, Michigan, from Thursday to Sunday, 6-9 June 1974. Co-hosts will be the Biological Station, the Michigan Audubon Society, and the Kalamazoo Nature Center. Detailed information about accommodations, transportation, field trips, and the Station will be sent to members with the advance registration forms and call for papers. Dr. Douglas James, Department of Zoology, University of Arkansas, Fayetteville, 72701, is program chairman and Dr. H. Lewis Batts, Jr., Kalamazoo Nature Center, 7000 North Westnedge Avenue, Kalamazoo, Michigan 49007, is chairman of the committee on arrangements.

The Biological Station, site of the Society's 1953 Annual Meeting, is a permanent field station for study, teaching, and research in the biological sciences, with special emphasis on interactions at various organizational levels and with application to human environmental problems. It occupies a 9,000-acre tract of wild land at the northern tip of Lower Michigan—about 25 miles south of the Straits of Mackinac and fewer miles from a major airport and an interstate highway. Most of the Station's 145 buildings are close to the 6½ miles of undisturbed shoreline lying within the boundaries of the Station and are near numerous other lakes, bogs, forests, dunes, marshes, and streams. Nesting areas of the Kirtland's Warbler are but 60 miles away and will be visited on a conducted field trip. Over 250 species of birds have been recorded in the area since the Station opened in 1909.

GENERAL NOTES

First record of Olivaceous Cormorants nesting in New Mexico.—During a 1972 survey of nesting birds at Elephant Butte Marsh, Sierra County, New Mexico, I found Olivaceous Cormorants (*Phalacrocorax olivaceus*) nesting in proximity with Double-crested Cormorants (*Phalacrocorax auritus*) and Black-crowned Night Herons (*Nycticorax nycticorax*). The marsh comprises inundated salt cedars (*Tamarix* sp.) and willows (*Salix* sp.), with about 550 pairs of Black-crowned Night Herons nesting in the salt cedars and 100 to 160 pairs of Double-crested Cormorants nesting in willow snags.

On 15 and 16 May 1972, four Olivaceous Cormorants were seen on nests at the marsh. Two of the nests were empty and two contained three eggs each. The nests, in slender willow snags, ranged from six to eight feet above water. A third empty nest nearby resembled the nests of this species in its situation and construction. On 23 May 1972, John P. Hubbard observed an additional Olivaceous Cormorant on another nest. When the marsh was revisited 16 and 17 June 1972, all of the nests of this species were empty. Failure of these nests, as well as all of those of night herons and most of those of Double-crested Cormorants, may have been due to hailstorms.

Several specimens of *P. olivaceus* have been taken in the state previously, two in the area of Cliff, on the Gila River, and at least two in the Rio Grande Valley near Hatch and Las Cruces; there is also an unverified record from the southeastern part of the state (Bailey, F. M., Birds of New Mexico, N. Mex. Dept. of Game and Fish, 1928). There are no previous records of the species nesting in the state. The birds seen by me and others in 1973 were smaller than *P. auritus*, with a distinct white border behind the gular patch. On 16 May 1972, identifiable photographs of an Olivaceous Cormorant were taken by Charles L. Hyder (now no. 121-1C in the U.S. National Photoduplicate file, Laurel, Md.). The eggs of the two species are similar in coloration, but those of *P. olivaceus* were smaller.

I am indebted to Jack Durham and the U.S. Bureau of Land Management for the opportunity to study nesting birds at Elephant Butte Marsh.—CHARLES A. HUNDERTMARK, JR., 305 Arvada N. E., Albuquerque, New Mexico 87102. Accepted 10 July 1973.

Foot injuries in Leach's Storm Petrels.—Deformities and injuries to beak and feet are occasionally seen when banding birds, a number of notes and review papers having been published on this topic (e.g. Pomeroy, Brit. Birds, 55:49-72, 1962). Previously, I recorded an injury to the foot of a Leach's Storm Petrel (*Oceanodroma leucorhoa*) (Canadian Field-Naturalist, 83:384-388, 1969) and suggested that it might have been caused by gulls (*Larus marinus* or *L. argentatus*) that were preying on the petrels. In 1970, 913 Leach's Storm Petrels were banded on Gull Island (47°15'N 52°46'W), the northernmost island of the three that form the Witless Bay Sea Bird Sanctuary, Newfoundland, and notes were made of any foot leg deformities or injuries. Forty-six birds (5.0 percent) were found to have foot leg injuries of varying degrees. In only two cases, however, were both feet legs of a single bird involved, Montgomerie (pers. comm.) noted foot leg injuries in 12 of 259 Leach's Storm Petrels (4.6 percent) banded in 1973, on Great Island, the southernmost island in the Witless Bay Sea Bird Sanctuary. Two of these 12 birds showed involvement of both feet legs. The number and extent of injuries recorded in birds from the two islands is detailed in Table 1, while Figure 1 shows some typical injuries.

The incidence of injury within the islands' colony appears to be approximately five

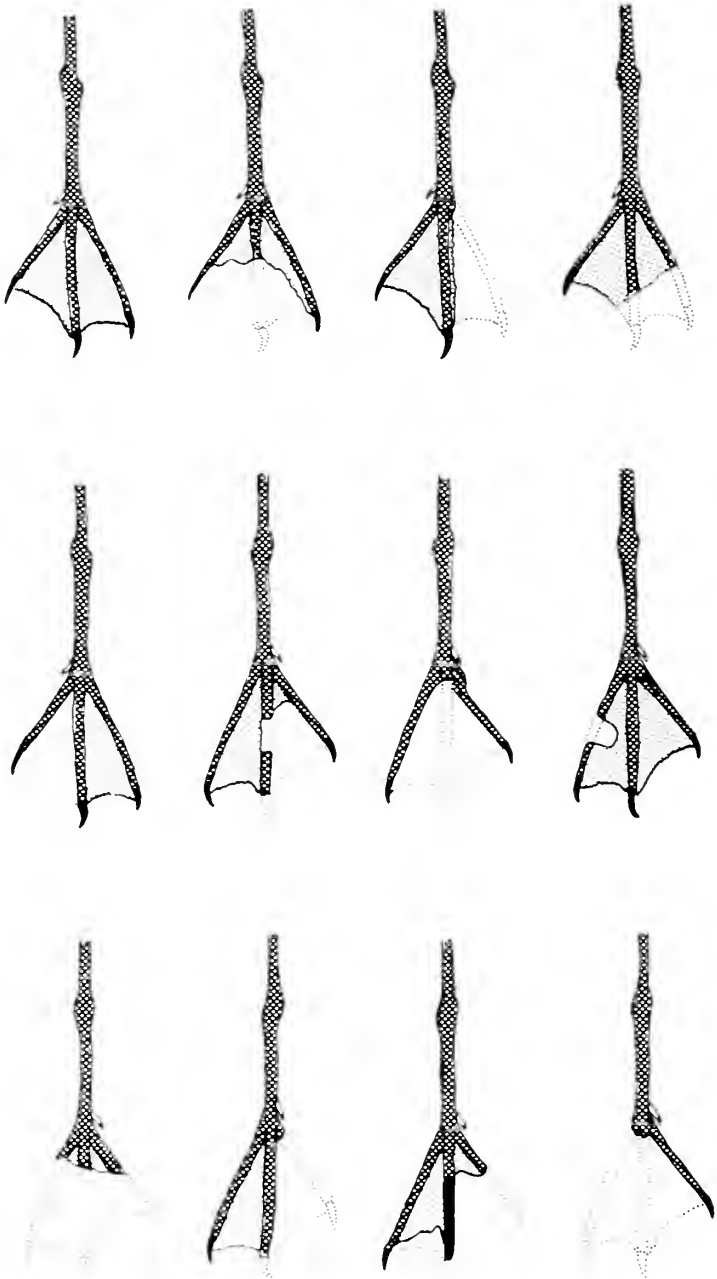


FIG. 1. Typical injuries to feet of Leach's Storm-Petrels, the dotted area being the missing portions.

TABLE 1
EXTENT AND NUMBER OF FOOT AND LEG INJURIES NOTED IN A SAMPLE OF 1172 LEACH'S STORM PETRELS

| Type of injury | Foot | | Comments |
|--------------------|------|-------|--|
| | Left | Right | |
| 1 toe missing | 4 | 13 | Whole or partial amputation, or small pieces missing, often some web damage. |
| 2 toes missing | 6 | 9 | Whole or partial amputation, including web damage. |
| 3 toes missing | 1 | 4 | Partial amputation, small portions of web remains. |
| Whole foot missing | 3 | 5 | Removed at joint or just distal to joint. |
| 1 web missing | 2 | 1 | |
| Tarsometatarsus | | | |
| Partially missing* | 5 | 2 | Stumps of various lengths remaining. |
| Tarsometatarsus | | | |
| Whole missing** | 1 | 1 | Amputated at tarsometatarsal tibiotarsal joint. |
| Deformed | 2 | 1 | |

* One specimen where leg (left or right) not specified in notes.

** One specimen where leg (left or right) not specified in notes.

percent and is most likely caused by gulls and or Common Puffins (*Fratercula arctica*). The latter are hole-nesters, and the petrels often start their own burrows in the entrance to puffin tunnels, perhaps to avoid having to dig through a tough, dense mat of grass-roots. In some cases, encounters may occur in the burrows between the two species and might result in injuries to petrels, particularly of the type where a small piece of toe or web has been "nipped" out (Fig. 1, middle row, far right). On the other hand, various colleagues have suggested that the injuries might have been caused by fish, when the birds were resting or swimming in the sea, although I prefer the gull puffin explanation.

Thanks are due to the National Research Council of Canada, for the grant (NRCC-A3500) that funded the fieldwork, and to John E. Maunder for all his help.—WILLIAM THRELFALL, *Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland. Accepted 13 October 1973.*

Snow Goose soaring with White Pelicans.—On 20 May 1972 at 11:00 we observed a flock of 21 soaring White Pelicans (*Pelecanus erythrorhynchos*) near the Delta Waterfowl Research Station, Delta, Manitoba. The flock was at an altitude of about 200–300 feet and moving toward the west. The day was clear and mild with little wind. As the flock passed, we noticed one bird considerably smaller than the rest, which examination with field glasses proved to be a Snow Goose (*Chen caerulescens*). As the pelicans soared and spiraled in normal flight, the Snow Goose seemed to have difficulty maintaining position within the flock. It flew at greater speeds and in larger arcs than the pelicans. As it approached the flock from the rear, it began shallow wing-beats in an attempt to

slow down. Invariably it would overtake and pass the flock, returning in a large arc to glide in from behind, only to repeat the pattern. At no time during our 10 minutes of observation did it abandon its attempt at gaining flock position. This incident took place over a week after the peak migration of Snow Geese through the Delta area. Apparently this bird was a straggler that for some reason did not continue migration with its own species.

Soaring by Snow Geese in conspecific flocks has been reported in the past. Williams (Condor, 44:76, 1942) observed 123 birds soaring near Brigham City, Utah, in October 1941. Sooter (Wilson Bull., 57:202, 1945) recorded 22 Snow Geese soaring on apparent rising air currents in February 1942 at Tulelake, California.

The incident at Delta is interesting in that the Snow Goose was attempting to emulate the typical flight pattern of a flock of another species. Evidently the pelicans produced the appropriate visual cues for the goose to identify with them. Both species are large white birds with black primaries. Perhaps the pelicans provided a supernormal releaser (Eibesfeldt, Ethology: The biology of behavior, Holt, Rinehart Winston, New York, 1970) to the Snow Goose, which would explain its persistence in attempting to fly with them in spite of apparent difficulties. One of us (B.D.J.B.) has frequently observed lone Snow Geese in association with flocks of Canada Geese (*Branta canadensis*). Since the Snow Goose is a polymorphic species with both a white and a dark (Blue Goose) phase, it would appear that the possible releaser stimulus for the species may be various large dark or white goose-like birds.—PATRICK J. CALDWELL AND BRUCE D. J. BATT, *Delta Waterfowl Research Station, Delta, Manitoba, Canada, RIN 3A1. Accepted 2 November 1973.*

A study of Mottled Duck broods in the Merritt Island National Wildlife Refuge.—This study, conducted in the Titusville, Florida area in the summer of 1967, was designed to investigate various aspects of brood survival and biology in the Florida race of the Mottled Duck (*Anas fulvigula fulvigula*).

Study Area.—The main study area consisted of spoil islands located in the Indian River and of mosquito control impoundments bordering the western shore of Merritt Island. The Indian River is a shallow estuary separating the island from the mainland; tides other than wind-caused are negligible. The mosquito control impoundments are bordered by a series of low dikes. Water levels fluctuate greatly, and the ponds commonly go dry during drought, as during the spring of 1967. At other times water may reach a depth of 3 feet or more, with rainfall the main source of water.

Vegetation within the mosquito control impoundments varies greatly. Saltgrass (*Distichlis spicata*) is common in all impoundments, and sawgrass (*Cladium jamaicensis*) is locally abundant. Other plants that are quite common include: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia nitida*), leatherleaf fern (*Acrostichum* spp.), cattail (*Typha domingensis*), sedges (*Cyperus* spp.), spikerushes (*Eleocharis* spp.), water hemp (*Acnida cuspidata*), hyssop (*Bacopa mennieria*) and rushes (*Juncus* spp.).

Hatching. Between 15 June 1967 and 5 September 1967, eight Mottled Duck nests were found on the spoil islands. Four clutches hatched, while two were abandoned and two were destroyed by predators. The time elapsing between the hatching of the first and the last young in a nest was found to be less than four hours. Females with their broods remained at the nest for eight to 15 hours after the first young hatched.

Movements of broods.—On the Indian River spoil islands, the movements of only two females with broods could be determined. In both cases, the females led their broods

towards the east (refuge) end of the island. These ducklings experienced much difficulty traveling through vegetation and often lost their balance. In one instance, a hen moved her brood approximately 100 feet in about seven hours.

Efforts to follow movements away from the islands were unsuccessful. A distinct possibility exists that these occurred at night. In several instances, broods known to be on the islands at nightfall could not be located there the following dawn. Circumstantial evidence seems to indicate that movements away from the islands take place within 24 hours of hatching, as no broods were found on the islands after that interval. Exactly where broods go after leaving the islands is unknown. Four broods were color marked but none of the ducklings was seen again.

Brood rearing habitat.—Night-lighting, ground surveys, and aerial surveys were all used to locate broods. Night-lighting was also used to capture ducks. When a brood was sighted, it was classified as to the stage of development according to the duckling classification system developed by Gollop and Marshall (Wildlife investigational techniques, Edward Bros., Inc., Ann Arbor, Michigan 1963). Broods consisting of young with down are classified as Class I, those with ducklings that possessed a combination of down and feathers are Class II, and those with young fully feathered but unable to fly are Class III.

All Class I brood sightings were made on the spoil islands, in or near nesting habitat. Most (72.7 percent) of the Class II broods were found in habitats characterized by either stands of saltgrass, interspersed with water not exceeding a depth of 12 inches and some mangrove, or in potholes 100 feet or less in diameter bordered by dense stands of cattail.

All Class III broods were found in habitats similar to those of Class II broods, but the former used more open water. This is reflected in open water frequency values of 18.2 percent for Class II broods and 38.5 percent for Class III broods. This may be an indication that as broods increase in age there is a tendency to move into more open marshes. Wright (High tide and an east wind; the story of the Black Duck, Stackpole Co., Harrisburg, Pa. 1954) observed a similar situation in Black Duck (*Anas rubripes*) broods.

Periods of brood activity.—The activities of broods were observed day and night with the exception of the period extending from 01:00-06:00. Peak periods of activity extended from 10:00 until 12:00, then tapered off until 14:00 when activity resumed and continued through early evening. The periodicity of brood activity at night was not clearly delineated.

Brood mortality.—There was a reduction in brood size with age of ducklings, i.e. 7.0 young per age Class I brood (average of seven broods), 6.5 per Class II brood (average of eleven broods), and 3.8 per Class III brood (average of thirteen broods). These figures were derived by dividing the total number of young by the total number of broods recorded for that age class. The sources of mortality were not discerned, but brood abandonment may have been a factor (see below).

Bond between the hen and her brood.—The strength of the bond between the female and her brood lessens as the brood grows older. The female was seen with her brood in 85.5 percent of all Class I sightings, 54.5 percent of the Class II sightings, and 38.5 percent of the Class III sightings. Females with newly hatched ducklings still in the nest were quite solicitous, flushing only when the vegetation covering the nest was parted. While observers remained near the nest the hen quacked loudly, performed a broken wing display, and swam about just offshore from the nest. In the cases of many Class II and III broods, the hen would fly off and leave the brood when startled.

Steiglitz and Wilson (J. Wildl. Mgmt. 32:921-924, 1968) found that 67.1 percent of Mottled Duck nests in the Merritt Island area are initiated prior to 16 April. My study was conducted during the latter part of the 1967 nesting season, and brood abandonment may account in part for the relatively low percent of Class II and Class III broods being seen with the female. Hochbaum (The Canvasback in the prairie marsh, Stackpole Co., Harrisburg, Pa., 1959) observed that a hen may remain with an early-hatched brood until it is ready to fly, while broods hatched later may be left when two or three weeks old or earlier. Early abandonment of late-hatched broods may also result in a greater mortality of such broods. Grice and Rogers (The Wood Duck in Massachusetts, Mass. Div. Fisheries and Game, Boston, 1965) indicated that only 22 percent of late-hatched Wood Ducks (*Aix sponsa*) reached flying stage, versus 66 percent in early-hatched individuals.

Sex and age ratios.—The sex and age of 70 Mottled Ducks captured by night-lighting or in wire traps were determined. The ratio of males to females in immatures was found to be 0.9:1 (in mature birds 1.3:1), while immatures outnumbered adults 1.72:1.

This research was financed by the Bureau of Sport Fisheries & Wildlife in cooperation with Tennessee Technological University. I wish to thank W. O. Stieglitz, C. T. Wilson, J. Carroll, D. Kosin, and S. Wineland for their assistance during the study. Appreciation is also extended to Dr. R. E. Martin, for his criticism, and to my wife, Donna Lynn, for her encouragement and help.—TERRY W. JOHNSON, *Department of Natural Resources, Game & Fish Division, Rte. 3, Forsyth, Georgia 31029. Accepted 29 October 1973.*

Aerial feeding by Snowy and Great Egrets in Louisiana waters.—Various aerial feeding methods have been described for the Snowy Egret (*Egretta thula*). The most common is hovering over shallow water, while stirring the water or raking the bottom vegetation with the feet, which has been described by Bond (Auk, 51:500-502, 1934), Grimes (Auk, 53:439, 1936), Meyerriecks (Wilson Bull., 71:153-158, 1959), and Sprunt (Auk, 53:203, 1936). Picking up food in direct flight has been reported by Dickinson (Auk, 64:306-307, 1947) and Jenni (Ecol. Monogr., 39:258, 1969), while Kushlan (Wilson Bull., 84:199-200, 1972) has described the taking of food in direct flight while the feet are dragged through the water.

In Barataria Bay, Jefferson and Plaquemines parishes, Louisiana, I observed on 32 occasions the hover method of feeding described for the Snowy Egret. The sightings were made from 24 May through 25 July 1972 and from 29 May through 26 July 1973. In these instances, the egrets were feeding on dead fish that were at or very near the surface in 4 to 5 feet of water. The egrets would pick up small fish with their bills while hovering over the surface of the water. On a few occasions the feet dangled in the water, but no stirring or foot dragging of the type described by the above authors was observed.

Groups of 12 to 120 Snowy Egrets were observed feeding on the dead fish discarded from boats trawling in the bay for shrimp. Feeding with the Snowy Egrets on these occasions were Great Egrets (*Casmerodius albus*), as well as Forster's Terns (*Sterna forsteri*), Royal Terns (*Thalasseus maximus*), and Ring-billed Gulls (*Larus delawarensis*). The Great Egrets flew 3 to 5 feet above the surface of the water, the legs horizontal and the head tucked back in the normal flying position, until a dead fish was sighted near the surface. On approaching the fish the egret would hover, extend the head downward, and pick the fish up with the bill. During this time the legs dangled beneath the egret, and the feet often dragged the surface of the water. The egrets would then fly upward and swallow the fish while in flight. This behavior was repeated many times by

individual birds. In a few instances, I observed Great Egrets picking up small fish in direct flight. In this method, the egret flew low over the water with the legs and head held in the normal flying position. Slowing its speed, the legs remaining nearly horizontal, the egret extended its head downward and picked up the fish.

Snowy Egrets always outnumbered the Great Egrets in these mixed aggregations, with a maximum ratio of one Great Egret to five Snowy Egrets in a flock. During my observation of hover feeding, I heard no vocalizations from either Snowy or Great Egrets. As indicated before, these mixed-species aggregations contained no other species of herons, although other species breed in great numbers with Snowy and Great Egrets on nearby islands. On two occasions, mixed flocks of egrets were seen to follow shrimp boats when the trawling nets were being cleared.

Snowy and Great Egrets nest commonly in the area where hover feeding was observed, and on a sunny day these white birds stand out for long distances against the background of a clear sky. Both species of egrets have been observed to fly from the vicinity of the breeding islands and join the feeding aggregations of egrets. On 4 June 1972, while I was on one of these islands, I watched a Great Egret leave the island and fly out to a mixed group of egrets hover-feeding approximately 1,500 feet offshore. Since there were no apparent vocalizations on the part of the actively feeding egrets, I am of the opinion that sight of the conspicuous white plumage serves as a signal indicating the presence of a readily available food source to Snowy and Great Egrets on nearby islands.—JAMES A. RODGERS, JR., *Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803. Accepted 10 September 1973.*

California Condor specimens in collections.—As part of a study of former numbers and distribution of the California Condor (*Gymnogyps californianus*), I have been able to locate 185 mounted birds and study skins, 51 skeletons, and 55 eggs of this endangered species. All but two skins and three eggs are housed in public or scientific institutions. United States collections contain 151 skins and mounts, 50 skeletons, and 52 eggs. In the following alphabetical-by-locality list, specimen numbers are listed in order: adult (A) and immature (I) plumaged skins or mounts skeletons eggs. I believe most specimens now in existence are included, and would appreciate learning of any additions.

AUSTRIA: Naturhistorisches Museum (Vienna)—2A,II 0 0; Oberosterreichisches Landmuseum (Linz)—1A 0/0. BELGIUM: Institut Royal des Sciences Naturelles (Brussels)—2A 0 0. CANADA: National Museum of Natural Sciences (Ottawa)—II 0 0; Royal Ontario Museum (Toronto)—1A,II/0 0. ENGLAND: British Museum (Tring)—7A, 3I 1 3. FRANCE: Museum National d'Histoire Naturelle (Paris)—2A,II 0 0. GERMANY: Zoologisches Museum (Berlin)—1A 0 0. MEXICO: Universidad Nacional Autonoma (Mexico City)—1A 0 0. NETHERLANDS: Rijksmuseum van Natuurlijke Histoire (Leiden)—1A 0 0. SWEDEN: Naturhistoriska Museum (Gothenburg)—2A 0 0; Naturhistoriska Riksmuseet (Stockholm)—1A 0 0. SWITZERLAND: Museum d'Histoire Naturelle (Geneva)—1A 0 0; Naturhistorisches Museum (St. Gallen)—1A,II 0 0. U.S.S.R.: Zoological Institute—Academy of Sciences (Leningrad)—2A,II 0 0. UNITED STATES, ARIZONA: University of Arizona, (Tucson)—1A/1 0. CALIFORNIA: Arthur Bryant Collection (Los Angeles)—1A 0 0; Bakersfield College (Bakersfield)—II 0 0; California Academy of Sciences (San Francisco) 12A,3I/1 1; Clarke Museum (Eureka)—1A,II 0 0; Fillmore High School (Fillmore)—0/1/0; Foster Bighorn Bar (Rio Vista)—1A 0 0; Fresno State College (Fresno)—1A 0 0; Kern County Museum (Bakersfield)—II 0 0; Los Angeles County Museum (Los Angeles)—10A,6I 10 1; Museum of Natural History (Santa Barbara)—3A,II 1 2;

Museum of Vertebrate Zoology (Berkeley)—4A,3I 12 2; Natural History Museum (San Diego)—4A 0 1; Pioneer Museum (Ventura)—II 0 0; Pomona College (Claremont)—II 0 0; San Bernardino County Museum (Bloomington)—II 0 1; Sidney Peyton Collection (Fillmore)—0 0 1; University of California (Los Angeles)—2A II 0; Western Foundation of Vertebrate Zoology (Los Angeles)—1A 0 7. COLORADO: Museum of Natural History (Denver)—5A,II 0 2. CONNECTICUT: Peabody Museum (New Haven)—1A 0 1. DELAWARE: Museum of Natural History (Greenville)—II 0 2. DISTRICT OF COLUMBIA: U.S. National Museum—8A,12I 9 5. FLORIDA: Florida State Museum (Gainesville)—0 0 2. ILLINOIS: Field Museum of Natural History (Chicago)—6A,II 0 7; University of Illinois (Urbana)—2A 0 0. IOWA: University of Iowa (Iowa City)—1A 0 0. LOUISIANA: Louisiana State University (Baton Rouge)—1A 0 0. MASSACHUSETTS: Museum of Comparative Zoology (Cambridge)—6A,8I 0 8. MICHIGAN: University of Michigan (Ann Arbor)—2A 0 0. NEBRASKA: Hastings Museum (Hastings)—1A 0 0. NEW YORK: American Museum of Natural History (New York City)—14A,7I 0 3. OHIO: Museum of Natural History (Cincinnati)—2A 0 0; Ohio State University (Columbus) II 0 0. PENNSYLVANIA: Academy of Natural Sciences (Philadelphia)—2A,2I 3 2; Carnegie Museum (Pittsburgh)—2A 0 1; Nelson Hoy Collection (Media)—0 0 1; Public Museum (Reading)—1A 0 0. TEXAS: Robert L. More Jr. Collection (Vernon)—0 0 1. VIRGINIA: Virginia Polytechnic Institute and State University (Blacksburg)—1A 0 0. WASHINGTON: University of Puget Sound (Tacoma) 0 0 1. WISCONSIN: Public Museum (Milwaukee)—2A,II 1 0. SANFORD R. WILBUR, *U.S. Bureau of Sport Fisheries and Wildlife, Patuxent Wildlife Research Center, 1190 East Ojai Avenue, Ojai, California 93023. Accepted 16 September 1973.*

Notes on prey and reproductive biology of Harris' Hawk in southeastern New Mexico. During the summer and early fall of 1973, I studied a small population of Harris' Hawks (*Parabuteo unicinctus*), about five miles northeast of Carlsbad, Eddy County. I gathered regurgitated pellets for the main food analysis and observed reproductive activity in five pairs or family groups on 23-24 May, 1-2 July, 30-31 July, 16-17 August, and 15-16 September, 1973. Pellet contents were identified with the aid of a dissecting microscope. Identification of mammalian skull remains was based on comparisons with specimens from the Museum of Southwestern Biology, University of New Mexico. Arthropods usually were identified by comparison with preserved specimens; centipedes (*Scolopendra* sp.) were identified from the mandibles. I also observed foraging activity of adults and food remains around nests and plucking areas.

Table 1 provides information on the prey of the hawk, as determined by methods given above. A significant finding was that invertebrates formed an important part of the diet, not just vertebrates as reported by Simmons (Birds of the Austin Region, University Press, Austin, Texas, 1925), Miller (Condor, 27:71-72, 1925), Bent (Life histories of North American birds of prey, Dover Publications, Inc., New York, 2:569-570, 1961), Hensley (Wilson Bull., 71:86-91, 1959), Le Sa-sier and Williams (Wilson Bull., 71:386-387, 1959), and Ligon (New Mexico birds, University of New Mexico Press, Albuquerque, N.M., 1961); apparently the studies of these authors were not based on pellet analysis.

Grasshoppers (Orthoptera) and beetles (Coleoptera) represent the majority of the invertebrate prey items. Wood-ticks were found in four pellets and always in association with ants, which were found in twelve pellets. One pellet contained 51 ants. The ants were distributed throughout the pellet and were both whole and as broken pieces (i.e.

TABLE 1
PREY OF HARRIS' HAWKS AS DETERMINED BY REMAINS IN 63 PELLETS

| Prey items in pellets | Pellets positive | Percent positive | Minimum number of individuals |
|-----------------------------------|------------------|------------------|-------------------------------|
| Vertebrates¹ | | | |
| <i>Sigmodon hispidus</i> | 6 | 9.5 | 10 |
| <i>Neotoma micropus</i> | 10 | 15.9 | 13 |
| <i>Neotoma albigula</i> | 3 | 4.7 | 4 |
| <i>Sylvilagus auduboni</i> | 13 | 20.6 | 14 |
| <i>Peromyscus</i> sp. | 2 | 3.2 | 2 |
| <i>Spermophilus</i> sp. | 1 | 1.6 | 1 |
| Invertebrates | | | |
| Beetles (Coleoptera) | 32 | 50.8 | 130 |
| Ants (Hymenoptera:Formicidae) | 12 | 19.0 | 95 |
| Bees (Hymenoptera) | 1 | 1.6 | 1 |
| Wood-ticks (Acarina:Ixodidae) | 1 | 6.3 | 34 |
| Centipedes (<i>Scolopendra</i>) | 6 | 9.5 | 8 |
| Grasshoppers (Orthoptera) | 17 | 27.0 | 32 |

¹All mammals, but also recorded as caught or as other remains were: *Phrynosoma cornutum* (Texas Horned Lizard)—1, *Geococcyx californianus* (Roadrunner)—3, and a quail sp. (Phasianidae)—1.

heads, abdomens, legs, etc.). It appears unlikely that this many ants would be picked up incidental to the eating of a prey item on the ground. Amadon and Brown (Eagles, hawks, and falcons of the world, McGraw-Hill Book Company, New York, 2:568-570, 1968) report that the Savannah Hawk (*Heterospizias meridionalis*), which they believe to be a close relative of *Parabuteo unicinctus*, eats ants and other insects. Centipedes (*Scolopendra* sp.) were found in six pellets from two different nests.

Cloudley-Thompson and Crawford (Exp. and Appl. Entomology, 13:187-193, 1970) report that scolopendramorph centipedes are primarily nocturnal. This, coupled with the remains of *Peromyscus*, suggests that these hawks are crepuscular foragers, a conclusion supported by my observations on 23 May. On that date a pair flew back and forth from the ground to a telephone pole between 20:00 and 21:00, until I could no longer observe them below the horizon with a pair of 10 × 50 binoculars.

Parmelee and Stevens (Condor, 66:443-445, 1964) observed copulation in this species taking place on the ground. I observed copulation in one pair five times, within a two and a half hour period, on 23 May and three times, during a two hour period, on 24 May. All eight copulations were above ground: two on a telephone pole, three on a fence post, and three on a mesquite (*Prosopis juliflora*) bush.

Elements of the pair-bond relationship were observed on 23 and 24 May. On the 23rd, between 08:00 and 09:00, the male of a pair fed the female small pieces of cottontail (*Sylvilagus auduboni*), as she sat on top of a telephone pole about 150 yards from the nest. The male crouched and fed the female two or three small pieces of meat at a time, after which he would crouch lower and scurry back and forth in front of her on the crossbar. On 24 May I saw the male catch a woodrat (*Neotoma micropus*), about

five minutes after the female had flown from her perch out of sight into lower mesquite brush, some fifty yards from the nest. The male carried the woodrat into the same area where the female had disappeared, and about fifteen minutes later he reappeared without the mammal.

Four nests were located, all in trees and at heights of about 25, 15, 10, and 6 feet above the ground. Cottonwood (*Populus deltoides*), mulberry (*Morus rubra*), and mesquite were used. Young fledged from two nests on or about 1 July. By using Bent's (op. cit. :143) incubation period of 28 days and a nestling period of 51 days (present study), I calculate that the eggs were laid about 12 April. Three other nests were at later stages than these two. On 1 July two nests with three eggs and one with two eggs were found. Both nests with three eggs had broken egg shells beneath them; thus the clutches may have been re-nestings. The young from these nests fledged young around 15 September. The two egg clutch failed to hatch. The only later clutch date on record, one on 25 August, was reported in Texas by Le Sasser and Williams (op. cit. :386).

On 16 August the bills of six young in two nests were covered with a white, salty (by taste) substance suggesting the presence of nasal salt glands.

I wish to thank B. E. Mattingly, Sam Crowe, and John Longmire for their assistance in the field and Dr. J. Ligon for critically reviewing the manuscript.—PETER H. PACHE, *Department of Biology, University of New Mexico, Albuquerque, New Mexico 87106. Accepted 15 November 1973.*

American Kestrel preys on least weasel.—On 11 January 1972, in south-central Ohio near the Ross-Pickaway county line, I observed a female American Kestrel (*Falco sparverius*) fly off a fencepost and drop a small mammal. I identified the latter as a female least weasel (*Mustela rixosa*). The skin of the weasel was torn off the head, and the neck was exposed and broken; otherwise the animal was intact. Captive and wild American Kestrels nearly always attack the head of a prey item first (Roest, *The Auk*, 74:1-19, 1957; pers. obs.). This suggests that the weasel was actually killed by the kestrel.

The least weasel is not included as a prey item of this species in a survey made by Heinzelman (*Wilson Bull.*, 76:323-330, 1964), and I could find no other records of its being taken by this kestrel.—G. SCOTT MILLS, *Department of Biological Sciences, University of Arizona, Tucson, Arizona. Accepted 8 November 1973.*

Feeding activities of Ospreys in Minnesota.—The breeding biology of Ospreys (*Pandion haliaetus*) has been studied extensively, but feeding activities are not well documented. Lambert's (Canadian Field-Naturalist, 57:87-88, 1943) study of fishing methods and success of Ospreys near Shelbourne, Nova Scotia, is one of the few published to date. My study presents information on fishing flights and methods, and food habits of Ospreys in north-central Minnesota in 1966 to 1971. The study area was in the Chippewa National Forest and included Itasca County, Minnesota. There are 1,217 lakes and 155 named streams totaling over 136,437 ha of water in the National Forest (Mathisen, *J. Wildl. Mgmt.*, 32:1-6, 1968), and much of the sparsely inhabited area is utilized only for logging and recreation.

The direction and destination of 41 fishing flights by male Ospreys from seven nests were recorded. Thirty-four flights from six of the nests to fishing sites were watched from blinds in trees along the flight paths in 1967. The other seven flights in 1971 from

two lakes to the seventh nest were monitored as the Osprey carried dead bluegills (*Lepomis macrochirus*) affixed with 4 to 10 g radio transmitters and left floating on the water (Dunstan, in press). Favored feeding perches were also located by monitoring such fish carried by Ospreys, and prey remains were collected from below these and nest sites. Whole or nearly whole remains were measured, weighed, and identified to determine species composition.

Fishing flights.—The average distance covered in all 41 fishing flights between active nests and fishing sites was 2.6 km. Flights from the six nests to lakes where fish were caught averaged 2.1 km. No correlation was noted between wind direction and velocity and distance or direction of fishing flight. Ospreys from five nests fished on two lakes and only one Osprey fished on one lake. Two males from two nests located 1.2 km apart fished on the same large lake, but in different parts of it. Ospreys rarely fished on the same lake at the same time, except at lakes of 5 ha or larger and never at the same location.

The fish marked with radio transmitters were carried to one nest from an average distance of 5.3 km. Five of the seven fish were taken from close to an active Bald Eagle (*Haliaeetus leucocephalus*) nest, and the Osprey's fishing range overlapped that of a pair of eagles (Dunstan, in press).

Harassment at fishing sites.—Ospreys chased Bald Eagles that perched near favored Osprey fishing perches and frequently stooped on Great Blue Herons (*Ardea herodias*) that walked the shore. Herons and eagles in flight were rarely harassed.

Fishing methods.—Ospreys watched for fish during flight and when perched. Soaring flights were made at heights of 30 to 200 m. Ospreys fished especially in this manner at larger lakes and those lacking sharp onshore dropoffs and trees along the shoreline, often visiting several in one flight. Birds stooped on half-folded wings to pick up live fish or with wings extended to pick up dead fish. H. R. Hanson (pers. comm.) twice watched soaring Ospreys swoop down and pick up floating, dead yellow perch (*Perca flavescens*) that had been left by fishermen.

Ospreys used a flapping flight primarily in the early morning and late evening (on windy or calm days) when they flew along shorelines searching for dead or dying fish washed ashore or entangled in offshore vegetation. Dead fish were picked up in swooping flight even on the shore. Centrarchid species were often selected while small cypriids, large suckers (*Catostomus* spp.), and northern pike (*Esox lucius*) were not. Twice Ospreys picked up dead northern pike that weighed more than 1 kg, only to drop them within 10 m.

Ospreys also fished by flying low over calm surfaces with the legs extended and feet dragging in the water, in a manner similar to the cooling behavior described by Abbott (The home-life of the Osprey. Witherby and Co., London, 1911). The feet were dragged intermittently for 30 to 60 m, disturbing the surface of the water and causing fish to move or jump. Fish disturbed in this way were then seized with one or both feet. Fish in shallow water over dense beds of coontail (*Ceratophyllum* sp.) usually tended to jump along the surface instead of swimming down into the weed mass. Ospreys flew back and forth over large weed beds for periods up to 30 minutes.

At lakes with steep onshore dropoffs Ospreys watched for fish from perches; they also made short flights along the emergent vegetation, dragging their feet for 2 to 10 m before returning to the original or nearby perch. After these flights they watched the area that had been dragged for fish that came to the surface. These were caught with a stoop. Crappies (*Pomoxis annularis*, *P. nigromaculatus*), bluegill, pumpkinseed (*Lepo-*

TABLE 1

THE NUMBER, PERCENT, AVERAGE LENGTH, AND WEIGHT OF 216 PREY REMAINS COLLECTED FROM BELOW FOUR FAVORED FEEDING PERCHES AND SIX ACTIVE NESTS

| Common name | Number | Percent | Length (cm) ¹ | Weight (g) ² |
|-------------------|--------|---------|--------------------------|-------------------------|
| Bluegill | 76 | 35.2 | 12.8 | 51 |
| White crappie | 7 | 3.2 | 18.3 | 77 |
| Black crappie | 67 | 31.0 | 17.2 | 82 |
| Yellow perch | 28 | 12.9 | 15.3 | 37 |
| Largemouth bass | 22 | 10.2 | 21.9 | 144 |
| Pumpkinseed | 9 | 4.2 | 13.2 | 54 |
| Northern redhorse | 4 | 1.8 | 27.0 | 612 |
| Northern pike | 3 | 1.4 | 42.8 | 624 |

¹total length tail compressed.

²weights varied due to stage of desiccation, decomposition, and missing tissue.

mis gibbosus), and largemouth bass (*Micropterus salmoides*) were attracted and captured in this way. These surface disturbances may have attracted the fish by their resemblance to floundering prey (fishermen sometimes deliberately stir the surface to attract the same fish).

The frequency of use of various fishing methods was influenced by weather and by the type of lake fished. Ospreys used the foot dragging method only over calm water. Because I could not maintain observation of individual birds for extended periods of time and over the extensive areas visited by them I was unable to gather good data on frequency of use of each method.

Prey species.—I found no prey other than fish. Fish taken as prey (and also most common in fishermen's catches, gill nets, and seine hauls) were: bluegill, white crappie, black crappie, yellow perch, largemouth bass, pumpkinseed, northern redhorse (*Moxostoma valenciennium*), and northern pike. Centrarchid species (crappies, bluegill, largemouth bass, pumpkinseed) composed 83.9 percent (181) of the prey found in or below four feeding perches and six nests (Table 1). Ospreys seldom took northern pike except during spawning or when found after winter- or summerkill. The average lengths and weights of prey remains are given in Table 1.

I gratefully acknowledge the constructive criticism given me by F. and F. N. Hamerstrom, Jr., J. E. Mathisen, G. A. Hall, and J. P. Hubbard during the writing of the manuscript. B. E. Harrell provided guidance during the study. Portions of this study were funded by a Chapman Memorial Fund Grant through the American Museum of Natural History, and the biology department of the University of South Dakota.—THOMAS C. DUNSTAN, *Department of Biological Science, Western Illinois University, Macomb, Illinois 61455. Accepted 25 September 1973.*

Clapper Rail in Tamaulipas, Mexico.—On 17 December 1938, George B. Saunders collected an adult male Clapper Rail (*Rallus longirostris*) in a brackish marsh, 10 miles south of the mouth of the Rio Grande, in Tamaulipas, Mexico. This specimen, now no. 532700 in the National Museum of Natural History, has recently been identified by me

as a representative of the subspecies *R. l. saturatus*. To my knowledge this is the first record of this subspecies in Mexico, and the first record of any Clapper Rail in Tamaulipas (Friedmann et al., Pacific Coast Avifauna no. 29, 1950; Dickerman, Wilson Bull. 83:49-56, 1971). The A.O.U. Check-list of North American Birds (1957) indicates that the range of *saturatus* extends along the coast of the Gulf of Mexico from Alabama to Brownsville, Texas. Whether this bird was a stray from slightly farther north or a member of an unreported resident population is not known, but there is no intrinsic reason why the range of this coastal subspecies should not extend beyond the international boundary.—RICHARD C. BANKS, *Division of Wildlife Research, Bureau of Sport Fisheries and Wildlife, Washington, D.C. (mailing address: National Museum of Natural History, Washington, D.C. 20560)*. Accepted 29 August 1973.

A possible "assist" to a hatching chick by an adult Whimbrel.—At the nest of a Whimbrel (*Numenius phaeopus*) under prolonged observation near Churchill, Manitoba, in July 1967, I observed a sequence of events that seem to represent an "assist" to a hatching chick by the incubating adult. The egg in question pipped about 48 hours prior to the "assist," during which time the other three eggs hatched and the chicks remained in the vicinity of the nest scrape. In the 39 hours after the egg first pipped, a crack about $\frac{1}{2}$ inch wide and halfway around the short axis of the shell developed. After 43 hours the adult Whimbrel moved the egg out of the scrape with a series of pushes from its bill, eventually leaving it about 8 to 10 inches from the nest. The bird pushed the egg about as far as it could stretch its neck without leaving the sitting position. The crack in the egg remained on top throughout this movement. The egg then remained outside the scrape in this position for 5 hours. From the blind I could see that occasionally the chick moved and the egg shook slightly. I could not hear any sound from the egg, but the wind was from the blind toward the scrape. After the 5 hour period the adult stood up and stepped over to the egg. Facing the scrape, the adult pushed and rolled the egg back to the nest: the egg rolled over completely once. The adult turned to face into the wind, started to sit down, but then stood again and very carefully inserted its bill into the crack in the egg, opening the mandibles as it did so. For about 2 minutes the adult repeatedly moved its bill along the crack, periodically opening the mandibles and seeming to pry at the crack during the process. The adult moved its body as well as its bill. After the "assist" the adult tucked the egg in with the chicks in the nest and sat down again. An hour later the adult took a single piece of shell out of the scrape and deposited it a short distance to the side. This piece of shell represented about a third of the long axis on one side and half on the other. After another hour, the adult stood up and walked off with this piece of shell. Then the bird came back, picked up another piece of shell from the scrape and flew off with it. This second piece of shell appeared to represent the reciprocal portion of the entire eggshell in comparison with the first fragment. Inspection of the nest during absence of the adult showed one wet chick and 3 dry ones. I left at that time, making a brief search of the area to which I had seen the adult carry the first shell fragment. I was not able to find it, so no inspection could be made that might have shown that the shell was abnormal in some way. A more extensive search was not made as this could have kept the adult from returning to brood the wet chick. The next morning 2 adults and 4 apparently normal chicks were in the area. Shell fragments were again sought, but could not be found.

I have never seen such a prolonged insertion of the bill into the crack of a hatching

egg by a shorebird, nor have I seen opening of the mandibles repeatedly in the crack of a hatching egg. It is not uncommon for an adult of many species of shorebirds to put the bill close in a sort of inspection of a hatching egg, but such inspections ordinarily last only 5 or 10 seconds and do not involve actual contact.—MARY M. TREMAINE, *Dept. of Medical Microbiology, University of Nebraska Medical Center, Omaha, Nebraska 68105. Accepted 18 September 1973.*

Sunbathing in the Streamertail Hummingbird.—Sunbathing is a widespread avian behavior, but is apparently unreported for the large New World family of hummingbirds, Trochilidae (Brit. Birds, 62:249-258, 1969). On 14 July 1973 I was taking feeding notes on birds in the Blue Mountains, Jamaica, at an elevation of about 5,000 feet, near Newcastle and the Clyde-dale Forest Reserve. At noon a male Streamertail Hummingbird (*Trochilus polytmus*), which had been foraging within 12 feet of me, perched in a small tree and began sunbathing. The bird widely spread the wings and tail (with the primaries almost touching the outer rectrices), holding them motionless and perpendicu-

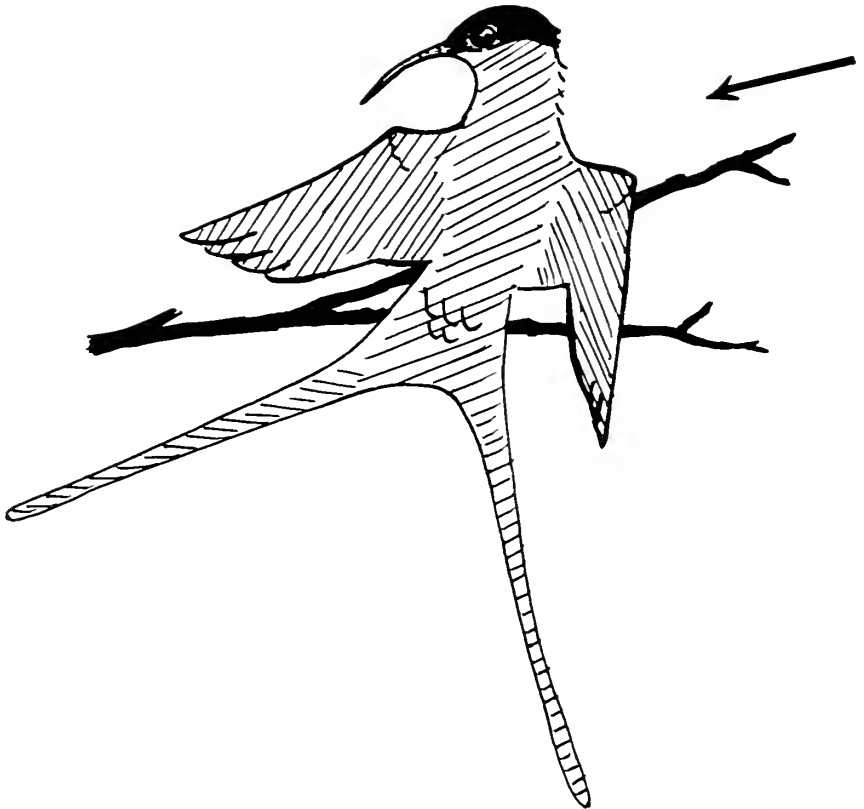


FIG. 1. Sunbathing posture of the Streamertail Hummingbird. The arrow shows the direction of the sun's rays.

lar to the sunlight (Fig. 1). The head was turned to the left with neck and body feathers fluffed, again maximizing incident radiation. The bird remained in this position for several minutes before resuming its foraging. While the bird was sunbathing I was able to approach it within several feet, and made a quick sketch of the posture.

This behavior may have been associated with the bird's "need" for additional heat absorption in the cool montane forest. Not surprising, in spite of hours of observation, I have not recorded the behavior in Streamertails of the warm lowlands. Other species of hummingbirds of high elevations may also engage in sunbathing and this should be watched for in the future.—CHARLES F. LECK, *Department of Zoology, Rutgers University, New Brunswick, New Jersey 08903. Accepted 23 July 1973.*

Aberrations in the tongue structure of some melanerpine woodpeckers.—In woodpeckers the tongue is a highly specialized apparatus, differing structurally, in certain respects, from that of most other families of birds. While the structure is mentioned in many ornithology texts, few detailed studies of it have appeared since Leiber's (*Zoologica*, 20:1-79, 1907) thorough treatise.

In the woodpeckers considered in this study, the two elongated hyoid horns, composed of the ceratobranchial and epibranchial bones, extend posteriorly from the posterior end of the basihyal, curving around the occipital region and roof of the skull and extending forward along the dorsal cranial surface toward the right nostril (Fig. 1A, B). Inserting on the distal tip, i.e. nostril end, of and completely surrounding each horn posteriorly is the branchiomandibularis muscle, which has its origin on the mandibular ramus. Upon contraction, this set of muscles pushes the tongue out of the mouth. In detail, the force of the muscles pulls on the distal tip of the hyoid horns which slide over the surface of the skull away from the nostril. The horn moves within a sheath of connective tissue which is normally attached to the rim of the right nostril. When the tongue is retracted the hyoid bones may extend within their sheaths into the right nostril in male birds. In females the horns may be somewhat shorter, terminating 6-10 mm short of the posterior margin of the right nostril.

In a recent study of the ecology and behavior of several species of melanerpine woodpeckers (Wallace, mss), I found that a surprising number of birds showed abnormal tongue development. The study involved examination of 14 males and eight females of the Red-bellied Woodpecker (*Centurus carolinus*), nine males and five females of the Golden-fronted Woodpecker (*C. aurifrons*) and four males and two females of the Red-headed Woodpecker (*Melanerpes erythrocephalus*), all from the North American mainland. Two island species were also studied: 15 males and 13 females of the Hispaniolan Woodpecker (*C. striatus*) and 15 males and 14 females of the Puerto Rican Woodpecker (*M. portoricensis*).

Examination included removal of the skin of the head to expose the hyoid horns and associated branchiomandibularis muscle. The abnormalities in every case involved the position or relative size of the epibranchial horns with their attached branchiomandibularis muscles. One of the more common aberrations involved horns of different lengths as illustrated in Fig. 1C and summarized in Table 1. Such relatively minor aberrations I have termed type I.

More pronounced aberrations included crossed horns (type II) and abnormal curvature of the horns with displaced attachment of the connective tissue sheath (type III), both shown in Fig. 2. Crossed horns were found in every species examined. In some such cases the horns were of different lengths, but neither horn predominated in being

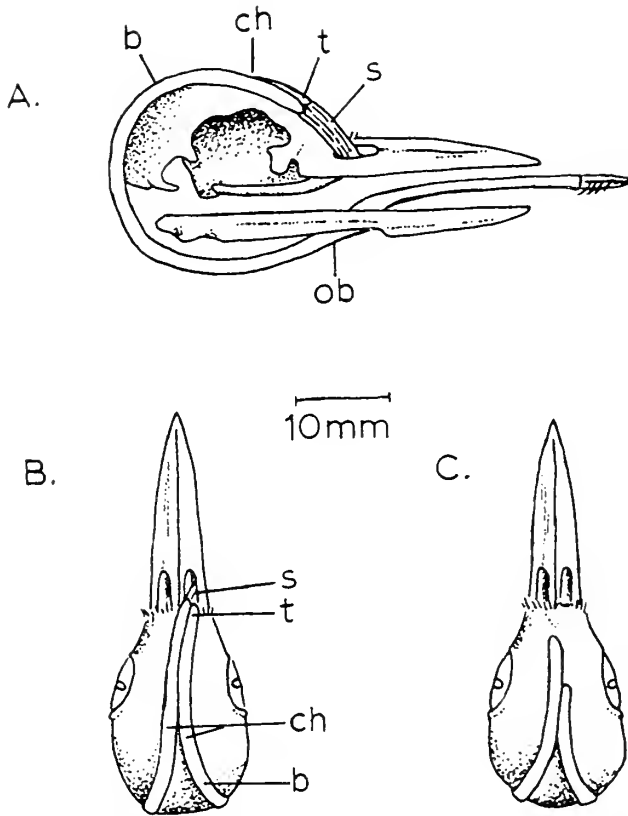


FIG. 1. A, B, normal structure of the tongue of the melanerpine woodpeckers included in this study. (Drawn from a male *Centurus striatus*.) ch, converging hyoid horns; b, M. branchiomandibularis; ob, origin of the M. branchiomandibularis; s, connective tissue sheath; t, tip of hyoid horns. The horns in some individuals may not extend into the nostril. C, type I abnormality, with horns of different lengths.

longer or above the other. I should note that if the tongue protruded at the time of collection, I pushed it back between the mandibles with the tip of the finger. On dissection, the membrane in which the hyoid moves over the skull was traced to its origin so that it was clear that the abnormal curvature was not artifactual.

Notably, type III aberrations (abnormal curvature of the horns) appeared only in the

FIG. 2. Types II and III abnormalities in woodpecker tongues. Top row, left to right: *Centurus aurifrons* male, female; *Melanerpes erythrocephalus* male; *C. carolinus* male. Middle row: *C. carolinus* male; *C. striatus* male; *M. portoricensis* male; male. Bottom row: *M. portoricensis* male, female, female, female.

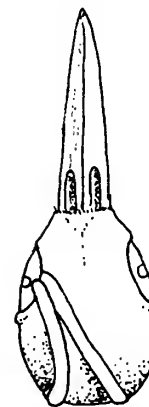
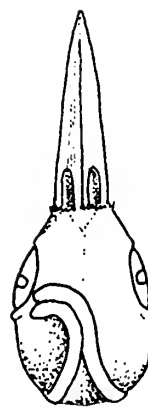
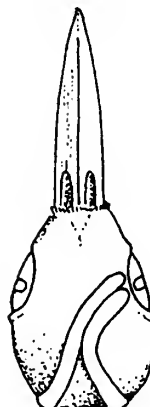
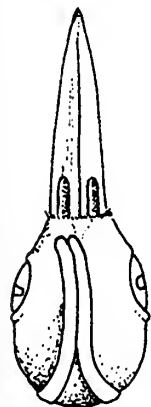
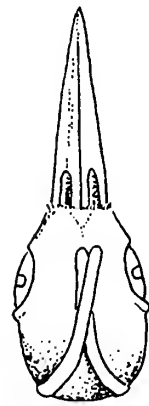
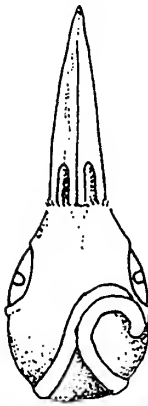
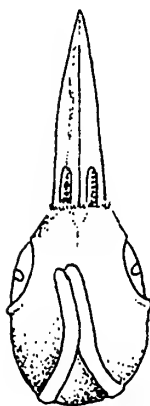
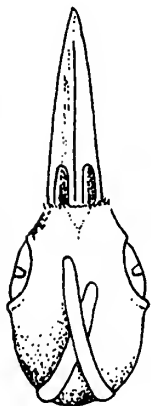
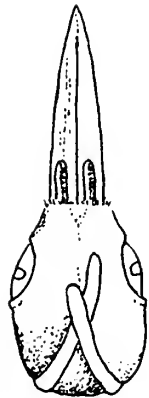
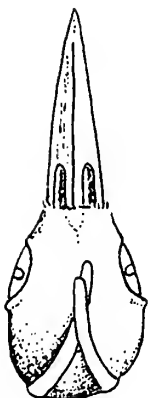
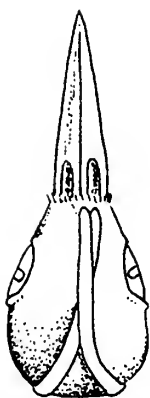
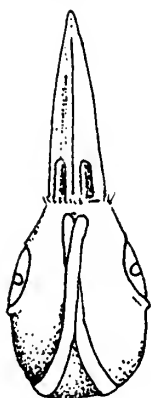


TABLE 1
SUMMARY OF TYPE 1 ABNORMALITIES

| Species | Sex | The longer horn | Termination ¹ | Difference ² |
|-----------------------------------|-----|-----------------|--------------------------|-------------------------|
| <i>Centurus aurifrons</i> | ♂ | R | 2 mm | 1.2 mm |
| <i>C. aurifrons</i> | ♂ | R | 2 | 1.3 |
| <i>Melanerpes erythrocephalus</i> | ♂ | R | 10 | 1.1 |
| <i>C. carolinus</i> | ♀ | L | 8 | 4.6 |
| <i>C. striatus</i> | ♂ | L | 9 | 6.9 |
| " " | ♀ | R | 12 | 4.1 |
| " " | ♀ | L | 8 | 6.4 |
| <i>M. portoricensis</i> | ♂ | R | 6 | 7.0 |
| " " | ♂ | R | 22 | 21.7 |

¹ Distance of origin of shorter hyoid horn from the base of the bill when the tongue is completely enclosed by the bill.

² Distance between points of origin of the two horns.

Puerto Rican species, which also showed a greater overall frequency (21 percent) of individuals with abnormal development than the mainland and the Hispaniolan species.

Why the Puerto Rican Woodpecker manifests an increased level of abnormality in tongue structure is unclear, but considering the incidence it seems that a certain level of variation from the norm is not strongly selected against. Increased variation in trophic structures has been demonstrated in several species of island birds, including woodpeckers (Selander, *Condor*, 68:113-151, 1966), and perhaps the tongue aberration in this case is associated with insularity. Definitive answers, however, await more specific data on the evolution and ecology of these species.

I express my appreciation to Walter Bock, Jack L. King, Lester L. Short, and Stephen Rothstein for their criticism and useful suggestions. The fieldwork was supported, in part, by a Frank M. Chapman grant from the American Museum of Natural History and a pre-doctoral research grant from the University of Texas at Austin.—ROBERT A. WALLACE, *Department of Biological Sciences, University of California, Santa Barbara, California 93106. Accepted 25 September 1973.*

A communal Common Raven roost in Virginia.—A nocturnal aggregation of at least 106 Common Ravens (*Corvus corax*) was observed roosting near Mountain Lake in Giles County, Virginia. This is the largest aggregation and the only communal roost known to be reported in the southern Appalachians. Wetmore (The list of birds of the Shenandoah National Park, Shenandoah Nat. Hist. Assoc. Bull., 1:12, 1950) observed a diurnal flock of more than 80 Common Ravens in Shenandoah National Park, Virginia, on 18 October 1947. Nocturnal roosts of Common Ravens have been reported in other parts of their range. Cushing (*Condor*, 43:103-107, 1941) reported a nocturnal roost of about 200 Common Ravens in the vicinity of Tomales Bay, California. Various authors in Great Britain have reported communal roosts, usually comprised of between 27 and 70 individuals, and on occasion up to several hundred.

The Mountain Lake roost was discovered shortly before sunset on 6 January 1973 when

a minimum of 62 Common Ravens was observed in the air simultaneously. The birds were soaring, sparring with one-another, and performing aerobatics prior to settling eventually into a clump of hemlocks (*Tsuga canadensis*). The high count of 106 ravens was established by photographs taken through a wide angle lens on 18 January 1973. A local resident reported that ravens have roosted in this vicinity in winters of previous years.—VINCENT J. LUCID AND RICHARD N. CONNER, *Division of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061. Accepted 13 September 1973.*

Predation on a shrew by an Eastern Bluebird.—On 23 July 1973, while making observations on the feeding behavior of a nesting pair of Eastern Bluebirds (*Sialia sialis*), near Mio, Oscoda Co., Michigan, the male was seen to capture and ingest a shrew (either *Microsorex hoyi* or probably *Sorex cinereus*). This unusual food item was obtained on a typical "drop" to the ground from a dead tree limb at 18:26. It was taken in the bird's bill to a fallen log where it was killed within 3 or 4 minutes. Subsequent preparation involved beating the prey against branches as the male held the lifeless shrew by its head. Twice the item was dropped, but on both occasions it was retrieved before it reached the ground. The bird changed limbs several times during preparation, appearing restless and seeking broader and more horizontal perches. As is typical for the bluebird the prey was always held and manipulated by the beak, never the feet, until it was finally ingested at 18:41.

During 30 minutes of observations prior to the capture of this food item the male fed his 8-day-old nestlings but once, although he foraged much for himself. After swallowing its prey the bird exhibited slight lethargy; his first trip to the nest with food was not until 18:56. During the 60 minutes following ingestion, 11 trips to the nest were recorded. Capture occurred at a time when insects appeared abundant and weather conditions (72°, sunny, light winds) were favorable.

Although the normal foods consumed by bluebirds are insects and fruits, Flanigan (Wilson Bull., 83:441, 1971) observed a female eating a snake about 8 inches long and Bent (U.S. Natl. Mus., Bull., 196:1949) reports finding a few bones of lizards and tree frogs in the stomachs of Eastern Bluebirds. While some insects consumed by this species are nearly equal in size to the shrew (e.g., Sphingidae adults, Mantidae, and Cicadidae), I could find no record of a bluebird feeding on mammalian prey in the literature. Of several thousand bluebird feedings observed by the author, this was unique and was not noted again during 3 subsequent days of observations on this pair.—BENEDICT C. PINKOWSKI, 8540 Hough, Almont, Michigan 48003. Accepted 4 September 1973.

Mountain Bluebirds nesting in North Dakota.—Although several specimens of the Mountain Bluebird (*Sialia currucoides*) have been taken in North Dakota, including in the extreme eastern portion, we have been unable to find any previous nesting record for the state. Bent (U.S. Natl. Mus., Bull. 196:286, 1949), on unspecified bases, gives the breeding range there as extending eastward to Fort Union, Arnegard, and Medora, all in extreme western North Dakota (the A.O.U. Checklist [1957] erroneously cites Fort Union as northeastern North Dakota.). On the J. Clark Salyer National Wildlife Refuge, McHenry County, in spring and early summer of 1972 and 1973, we found Mountain Bluebirds moderately common in sandhill-grassland-aspen parkland, habitat typical of the southern one third of the refuge, and found two nests.

In 1972, Mountain Bluebirds were first observed at the refuge on 11 March. On 31 May, a pair was observed carrying food, largely insects, to a nest hole about four meters up in a dead aspen (*Populus tremuloides*). On 5 June we spent several hours observing and photographing the pair in such activity. On 22 June, adults were seen in the vicinity and we inspected the nest, but the young were gone. This hole was not occupied in 1973.

In 1973, bluebirds were first observed at the refuge on 13 March. A nest hole about three meters up in a dead aspen was found on 27 May, in a heavily wooded area about two miles from the 1972 nest site. The pair of bluebirds was observed carrying insects to the hole at about five minute intervals. On 31 May, we saw four well-feathered young in the nest. On 3 June the adults were still feeding the young in the nest.

A check of refuge records revealed initial spring sightings of Mountain Bluebirds on 27 March 1971, 21 March 1970, and 23 March 1969. Prior to 1969 no detailed records were kept on songbirds, but occasional sightings go back to 1936, when the refuge was established. Mountain Bluebirds have been nesting on the refuge since at least 1972 and probably earlier. These data thus extend the known breeding range of this species some 150 miles farther east than previously reported, i.e. from western South Dakota (Visher, *Wilson Bull.*, 24:1-6, 1912).

We wish to thank Dr. Harrison Tordoff and Joseph Wunderle, Jr., who read the manuscript.—HENRY KERMOTT, *Department of Ecology and Behavioral Biology, Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 55455*; ROBERT FIELDS and ALAN TROUT, *Bureau of Sport Fisheries and Wildlife, J. Clark Salyer National Wildlife Refuge, Upland, North Dakota 58789*. Accepted 23 October 1973.

Unusual crepuscular blackbird movements.—At approximately 18:30 on 28 and 29 February 1972, we observed long flight lines of blackbirds, mainly Red-winged Blackbirds (*Agelaius phoeniceus*), leave a long-established winter roost at Milledgeville, Baldwin County, Georgia, and fly out of sight in a northwesterly direction. An estimated 3,000 birds were seen leaving the first evening and 5,000 the second night. On both nights, the birds had arrived at the roost within the previous hour, sunset was at 18:32, there was virtually no wind, the sky was clear, and a full moon had already risen when the birds left. There was no other known roost north, northwest, or west of the Milledgeville roost that the birds could have reached before dark. We remained at the roost most of both nights and, to the best of our knowledge, the birds did not return.

Our observations were made as part of a test of bird responses to scaring devices conducted at the Milledgeville roost. The test included the use of one or more devices (i.e. recorded alarm cries, Av-alarm, exploding shotgun shells) once every 15 minutes during 8-hour periods on the nights of 24-26 and 28-29 February. To what degree the scaring activity was connected with the observed exits from the roost on 28 and 29 February is not known. While we were in plain view of the birds as they arrived at and then departed from the roost, we had not yet begun our scaring activities either night. The estimated roost population decreased from 40,000 to 2,500 birds between 24 February and 1 March.

To our knowledge, no other workers have reported concerted movements of this type from a roost at dusk. When roosting blackbirds are harassed at night, they usually will fly out in loose, unorganized masses and will settle down again rapidly in nearby vegetation. This may have been a local movement, but if so it resulted in a shift to a new and unreported roost site.

The possibility exists that the movement may have been the beginning of nocturnal

migration, although no such phenomenon in blackbirds has ever been reported to our knowledge. The birds were headed in the proper direction, and blackbird movements north occur regularly at this time (vanguards of the Red-winged Blackbird migration normally reach northern Ohio about 1 March). Stoddard and Norris (Bird Casualties at a Leon County, Florida TV Tower: An Eleven-year Study, Bull. Tall Timbers Res. Stn. No. 8:90, 1967) report many dead Redwings in the early morning at a TV tower in northern Florida. However, they believe that these birds likely struck the tower and attendant guy wires under crepuscular rather than nocturnal conditions.

We thank Judge Erwin Sibley for allowing our use of the roost on his property for studies and J. S. Webb and W. J. Francis for reviewing this note.—ALLEN R. STICKLEY, JR., *U.S. Bureau of Sport Fisheries and Wildlife, Division of Wildlife Research, Patuxent Wildlife Research Center, Ohio Field Station, P. O. Box 2097, Sandusky, Ohio 44870* and DAVID E. STEFFEN, *129 Collumer Road, Hilton, New York 14463. Accepted 7 September 1973.*

Common Grackles preying on fish.—In June 1973, I observed Common Grackles (*Quiscalus quiscula*) preying on small fish at the spillway of Bluff Lake, Noxubee Wildlife Refuge, Oktibbeha County, Mississippi. Up to 15 birds engaged in the behavior, feeding sporadically and with neither great agility nor awkwardness on small minnows of unidentified species. I observed the activity for two hours on 23 June and four and one half hours on 24 June, while sitting 50 to 150 feet away and using 7× binoculars. On 25 and 27 June I also noted that the birds were feeding at the spillway, which empties from the lake into Oktoe Creek. On these dates water running over the spillway was one to two inches deep, but on 29 June the spillway was dry and no grackles were in it.

When feeding in the spillway, birds would alight on a nearby perch or land directly in the water. Perching birds flew down to the water and caught fish, while those in the water walked around and caught fish that happened to be swept near them. A captured fish was frequently eaten immediately after being caught, either as the bird stood in the water or after it flew to a tree branch or the concrete wall of the spillway. Most of the time the grackles ate fish whole, head first. On some occasions a grackle held a fish with its feet and tore out small pieces to eat.

Some grackles did not eat the fish at the spillway, but left with them in their bills and may have taken them to nests or young. Such birds carried away up to three fish at a time. In one incident, such a bird held the first fish that it caught under its foot while it caught a second one. It then flew away with both fish in its bill.

A young grackle also came to the spillway and was repeatedly fed whole fish by an adult. The young bird made no attempt to catch fish and was very vocal until it was fed. It was quite clumsy with the fish, usually dropping them two or three times before swallowing them.

Common Grackles have previously been reported to eat small fish and feed them to their young. Beal (U.S. Dept. Agri. Biological Survey, Bull. 13, 1900) and Snelling (Auk, 85:560, 1968) report occurrences of fish in gullet and stomach analyses, but it was not known if the fish were taken alive. Beal states that fish were infrequent in nearly 2,500 stomachs.

Snyder (Canadian Field-Naturalist, 42:44, 1928) describes Common Grackles fishing for small minnows in a garden pool in Canada. He presumed the adults were carrying the fish to the young, although he saw no actual feeding taking place. Pellett (Wilson Bull., 38:235, 1926) describes similar behavior by Common Grackles below a dam near

Hamilton, Illinois. He did not see fish eaten but presumed also that the birds were feeding them to young. In contrast to my observations, he observed the grackles "beating the minnows to death," before carrying them away.

I wish to thank Dr. Jerome A. Jackson for his suggestions and encouragement concerning this manuscript. This note is a result of a project for an ornithology course in the Zoology Department at Mississippi State University.—TOM DARRIN, *546 Moss Hill Drive, New Albany, Mississippi 38652. Accepted 12 November 1973.*

ORNITHOLOGICAL NEWS

We saddened to note the passing of Albert F. Ganier in Nashville, Tennessee, on 20 December 1973. Mr. Ganier was the Society's oldest living president, having served from 1924 to 1926, and he joined the Society in 1915. We also note the passing in recent months of Amelia Laskey and the Rev. Joseph James Murray, both of whom were contributors to the Bulletin and the Society.

Limited funds are available through the National Academy of Sciences for travel to the International Ornithological Congress in Canberra, Australia in August, 1974. Selection will be made by a panel of the U.S. National Committee of the International Union of Biological Sciences. Direct inquiries about application for the funds to Mr. Harvey Sheppard, Division of Biological Sciences, National Research Council, Washington, D. C. 20418. Application should be submitted by May 1, 1974.

The International Council for Bird Preservation has funds for research and conservation of endangered or vulnerable species. Proposals may be submitted to the Office of the President, I.C.B.P., Room 336, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, U.S.A.

I.C.B.P. is currently revising the Red Data Book, Vol. II, Aves, on agreement with I.U.C.N. Published or unpublished reports on the status of endangered or vulnerable bird species are urgently requested at the above address.

THE PRESIDENT'S PAGE

For the 75th anniversary volume of *The Wilson Bulletin*, I compiled a checklist of the species of birds that had been portrayed on colored plates in our journal through 1962, as well as a list of the artists and photographers whose work had been so reproduced (Wilson Bull., 75:289-294, 1963). Whoever prepares a supplement to this list for our centennial volume in 1988 will have an exciting task. In the volumes from 1963 through 1973, we published fifteen paintings and five photographs in color. Now, through the generous gift of Dr. George Miksch Sutton as announced in the December 1973 issue, we have an endowment that will enable us to publish as many as four colored plates each year.

In my 1963 article I emphasized the high cost of color reproduction and the limited budgets of journals in advocating severe selectivity in choosing paintings or photographs. The fact that Dr. Sutton's endowment has freed us from the financial strictures should not warrant any relaxation of our standards of selectivity. As I wrote in 1963, "[A colored plate] should not be published merely as an attractive picture, but should make some point; it should illustrate something that *needs* illustration. . . ." There is now very little justification for our publishing more photographs, much less paintings, of familiar North American birds unless they make some biological point: a little-known plumage stage, for instance, or a display posture. The traditional parent-at-the-nest photograph is, of course, still welcome if the subject is as unfamiliar to most of us (at least on the breeding grounds) as the Smith's Longspur and Stilt Sandpiper, two species that have figured in recent photographic frontispieces.

Especially exciting for both authors and readers is the prospect, now feasible, of *commissioning* colored plates to accompany articles that virtually cry out for such illustration. The frontispiece in this issue is an example; unlike the Blue-winged Golden-winged Warblers, the Baltimore Bullock's Orioles, or the Indigo/Lazuli Buntings, the intermediate phenotypes of the Rose-breasted/Black-headed Grosbeaks had never been figured in color. It was obvious to the Editor that Dr. Anderson's paper would be even more valuable if accompanied by a colored plate, so Mr. Sandström was provided with selected specimens from which to paint. Other such commissioned plates are already in prospect.

If readers of *The Wilson Bulletin* have been fortunate enough to obtain really good photographs of little-known species that have seldom (or never) been illustrated in color, they should consider submitting one or more of these as potential frontispiece plates. If the photographer's field experience with the species has been limited, the editor can solicit a brief article to accompany the photograph from an author who knows the bird well. Just such a photograph/article combination will appear later this year in *The Wilson Bulletin*, the subject being the endemic ibis of Madagascar, *Lophotibis cristata*.

I am happy to report that Don R. Eckelherry and Olin Sewall Pettingill, Jr. have agreed to act as advisors to assist the Editor in finding suitable paintings and photographs, respectively, and in evaluating those submitted for possible publication. We hope that authors, artists and photographers will keep in mind the opportunities to enhance our journal opened up to all of us through Dr. Sutton's devotion to the Wilson Ornithological Society.—KENNETH C. PARKES

ORNITHOLOGICAL LITERATURE

AVIAN BIOLOGY, Volume I. Edited by Donald S. Farner and James R. King. Academic Press, Inc., New York, N. Y., 1971: xx + 1-586 pp., many charts, drawings, and photographs. \$30.00.—This is the first of a projected four volumes compiled to "provide a reasonable assessment of selected aspects of avian biology" in the early 1970's. The series is stated to be a direct descendant of the late A. J. Marshall's two volumes, *Biology and Comparative Physiology of Birds* (1960), and the expansion of knowledge and development of new perspectives are given as justification for the proliferation of topics in this series.

The emphasis in this volume is broadly evolutionary and ecological. The ten authors represent not only competence in their specialties, but, collectively, a world view of avian biology in terms of their national origins, training, and field experience. An innovation for a work of this sort is the designation of a Taxonomic Editor, Kenneth C. Parkes, to monitor problems of uniformity in the designation of species.

In the initial chapter, Robert W. Storer reviews the problems of classification and discusses recent developments in the allocation of selected groups. He presents a classification of birds that is more or less traditional, departing from the Wetmore order where new evidence has accumulated (e. g., transfer of the sandgrouse to the Charadriiformes). A superordinal segregation of the penguins is abandoned, and *Ichthyornis* transferred to a list of forms of uncertain taxonomic status. The list is synoptic in form, and includes 97 non-passerine and 58 passerine families, in comparison to 100 and 61, respectively, in his 1960 list. Six songbird groups recognized as families have been demoted and five other passerine groups elevated to family level. More important than these numbers in providing clues to activity in classification in the preceding decade is the wholesale change in the order of listing of passerine families. The corvine assemblage is shifted nearer the end, and the Icteridae is listed last. A divergence of views is evident when Storer's treatment of Mesozoic fossil groups is compared to that of Pierce Brodkorb (Chap. 2). Storer is more cautious about linking fossil groups to extant taxa.

Brodkorb reviews reptilian predecessors of birds and presents a detailed analysis of the structure of *Archaeopteryx*, in which he recognizes two species. He compares limb proportions to those of a touraco, a chachalaca, and the hoatzin, in an effort to deduce the locomotor patterns of the earliest known bird. His conclusion that *Archaeopteryx* "probably ran agilely along the branches" seems uncontested, but the statement that flight included flapping is at variance with deBeer's interpretation (pp. 58-62 in A. L. Thomson, *A New Dictionary of Birds*, 1964). Brodkorb attempts to reconstruct avifaunal composition in time; his table reflects the major radiation of families in early Tertiary, but, surprisingly, suggests the presence of passerine families in later Cretaceous when the number of contemporaneous species is estimated at fewer than 1000.

The chapter on Adaptive Radiation in Birds (also by R. W. Storer) has stood the test of time, being little modified from the 1960 version. Details concerning groups known only as fossils have been reassigned to Brodkorb, and a section on radiation in the Charadriiformes has been added. Several of the photographs were much sharper in the 1960 version, owing, perhaps, to the better quality of paper used in that volume.

Robert K. Selander presents a comprehensive and perceptive review in "Systematics and Speciation in Birds," distinguishing throughout between systematics ("the study of the kinds and diversity of organisms and the relationships among them") and taxonomy ("the theory and practice of classifying organisms."). He comments critically on the

references cited, and emphasizes the advances to be gained through the use of newer techniques and concepts, such as the weighting of hybrid indices. With reference to the acquisition of isolating mechanisms, he urges "a strongly statistical approach to the problem of the degree to which interactions of semi-species and species affect the evolution of [those] species differences that promote genetic isolation and ecological compatibility." I found certain of the figures in this chapter difficult to read. Shading of land areas in maps of archipelagoes and the expansion of legends in other instances (figure 31) would have facilitated the reading of this otherwise lucid account.

The late R. H. MacArthur, in "Patterns in Terrestrial Bird Communities," considers spatial and temporal organization and interspecific associations. He covers the requirements for coexistence, and demonstrates that theoretical approaches can direct the observer to the appropriate correlated measurements to make in studies of niche overlap.

Two chapters that follow deal with the responses of birds to environments that are challenging to birds and present great diversity on a global scale: N. P. Ashmole's "Sea Bird Ecology and the Marine Environment" and D. L. Serventy's "Biology of Desert Birds." Ashmole incorporates recent oceanographic advances, considering the influences of surface temperatures, salinity, cycling of nutrients, and convergences of masses of unlike waters on primary production and bird distribution. He classifies foraging methods of sea birds, relating the geographic differences to latitudinal and seasonal contrasts in the richness of the areas. He observes that in polar and subpolar waters most sea birds feed on rather passive prey taken at or near the surface, although fishes are important prey over the continental shelves. In low latitudes pelagic and offshore feeders forage by dipping and plunging; vertical migrations of prey organisms (chiefly flying fishes and squid) are important in such waters. A picture that emerges from his account is one of a shelterless environment in which certain tropical sea birds are forced to modify their foraging methods (dipping rather than plunging) while over the schools of predatory fishes upon which they rely to drive their prey to the surface.

In contrast to the highly synchronized and seasonally restricted breeding schedules of higher latitudes, Ashmole suggests that the onset of breeding in many tropical sea birds is regulated by the individual acquisition of sufficient energy reserves. The high rates of adult survival of marine birds are examined, and a variety of mechanisms for the regulation of numbers postulated. Geographic (latitudinal) replacement of related forms is attributed to the difficulty of establishing reproductive isolation rather than to competitive effects in achieving sympatry.

Serventy presents a comparative study of deserts, defining them by the moisture index of Thornthwaite. He concludes that the questions of geologic age and persistence of deserts are still to be resolved, and he rejects the view that North American deserts are younger than those of the Old World. Avian desert specialists (defined by distributional criteria) make up only a small percentage of any of the continental avifaunas, and the evolution of desert adaptations is judged to have been retarded by climatic fluctuations that may have eliminated some aridity refuges. Both the pallid and black coloration of desert birds are attributed to selection for crypticity, the black coloration contributing to the elimination of shadow and conferring a metabolic advantage under cool temperatures.

Serventy points out that breeding seasons are least regular in the Australian deserts (a highly erratic environment), fostering not only opportunistic breeding but nomadism that is little evident on other continents. Some Australian desert birds are notable for the extent of overlap in breeding and molt. The chapter concludes with comprehensive

reviews of behavioral and physiological responses to the distribution of water and of heat regulation in desert birds.

Certain of these topics are expanded in Klaus Immelman's "Ecological Aspects of Periodic Reproduction." This author observes that reproductive seasons must be timed to periods of minimum stress on adults, as well as to optimal conditions for the offspring, and he provides a wealth of data on breeding cycles other than those that recur on an annual basis in the life of the individual. In his discussion of ultimate factors, Immelman documents pressures other than the availability of food that influence the onset of breeding; included are interspecific competition (*contra* Slud, *Auk* 81:444-446, 1964), nesting conditions, predation pressure and climatic factors. Apart from the Short-tailed Shearwater, endogenous controls of breeding cycles remain to be demonstrated. The precise mechanism of the stimulus of rainfall in the initiation breeding activity has not been ascertained. The responsiveness to several kinds of controls, and the "safety mechanism" of postnuptial refractoriness are considered to have evolved independently in different groups. The lack of experimental evidence is cited repeatedly by Immelman.

Lars von Haartman deals with, in "Population Dynamics," a wealth of experience in long-term field investigations in northern Europe, where the impact of winter temperatures on bird numbers is more noticeable than in Britain or Germany. His search for factors other than food in elucidating habitat selection, carrying capacity and functions of territory is refreshing. His view of bird numbers in forests and lakes is enriched by many citations from European journals, and he concludes that population levels in a number of species discussed fluctuate within limits characteristic for those species. Von Haartman reiterates his earlier view that non-breeding can act as a density dependent check on increase in numbers (a thesis supported by Ashmole, p. 267), and he develops the attitude that population dynamics consists of more than a balance between natality and mortality. He concludes that factors regulating clutch size still are unexplained, and demonstrates density dependence in the mortality of both independent juveniles and adults.

In contrast to von Haartman's empirical approach, Martin L. Cody uses demographic theory in examining "influences of environmental factors on the various life-history parameters that determine reproductive rates." Cody develops the concept of reproductive commitment ("the sum of efforts put directly into production of offspring"). In the early stages of population growth or when the prospects of an individual's surviving to breed again are low, commitment is expected to be large and to begin at an early age. Such a pattern characterizes many land birds of the temperate zone. A shift in strategies should occur as the growth phase ends, i.e., when a greater premium is to be placed upon defense of resources and the spread of the commitment over a longer time span becomes advantageous. Such a pattern often is found in marine birds and tropical (land) species.

Cody interprets the association of smaller clutch size and lower latitudes as a case of reduced reproductive commitment in response to a greater predictability of the environment. He argues that, since the population is merely replacing itself under such conditions, survival of adults will be enhanced, whereas fewer of their offspring will survive to enter the breeding population and will do so at a later age. Large losses of eggs and young to predators will further contribute to reduced size of commitment (= clutch). Thus, where adult survival is high and breeding success low, small clutches will be repeated through a longer life span. In his review of reproduction in other geographical gradients and of reproductive patterns on islands, Cody finds little support for Lack's food-scarcity hypothesis. Although the relationship in his Figure 4 ("breeding success

verus (*sic*) adult survival") would not be altered. Cody is in error in stating (p. 490) "in Song Sparrows and parids over 70% of the adults die each year." The reference paper cited as "R. E. Johnson, 1960" (p. 495) can be located by the volume number of the journal cited.

In his brief "Ecological Aspects of Behavior," Gordon Orians applies optimality theory to problems such as foraging behavior, habitat selection, patterns of spacing, and the evolution of polygyny. He analyzes territorial behavior in economic terms, and points to the quantification of the relationship between territory size in different habitats and food availability and its assessment by the birds as a direction for future research.

Some of the topics considered in this volume lend themselves to more than an up-to-date summary, and Selander, Immelman, Cody and Orians are to be commended for emphasizing specific subjects that demand further study. The volume is indexed separately by author, bird names and subject. An expansion of the last would have been helpful in view of the unavoidable overlap in certain topics. For example, there is one entry for "body size," a subject dealt with in a substantial way in three other chapters. Although the standards of editing and production are high, the price of this volume impresses me as excessive. Because of its importance, the active investigator or teacher has no recourse, but he can avail himself of a modest saving in the subscription rate for the four volumes.—KEITH L. DIXON.

THE BIRDS OF BRITAIN AND EUROPE WITH NORTH AFRICA AND THE MIDDLE EAST. Illustrations by Hermann Heinzel, text by Richard Fitter, maps by John Parslow. J. B. Lippincott Co., Philadelphia, 1972: 336 pp. \$7.50. THE OXFORD BOOK OF BIRDS, POCKET EDITION. Text by Bruce Campbell, illustrations by Donald Watson. Oxford University Press, New York, 1972: xvi + 207 pp. \$5.00.—I was incredulous on hearing that two new field guides to British and European birds had just been published. Could it really be true that some of Europe's top artistic and writing talent had been siphoned off into putting out yet *another* European bird guide? Come on! It is indeed true, but the books are not as redundant as they seemed. One covers other areas besides Europe, while the second is only new in the sense that it is a smaller edition of an already published work. Nevertheless, the question must occur to the owner of one of the many extant guides to British and European birds—"why should I buy them?"

My first reaction when I started reviewing these books was that I developed a case of eyestrain. The print in the Lippincott book is so small that I had to pause frequently to rest my eyes. Hoping for relief, I turned to the Oxford book, only to find that its print was even smaller; I literally had to use a magnifying glass to read it. The idea of a pocket field guide is great, but not at the cost of ruined eyesight.

The original *Oxford Book of Birds* was published in 1964 and was reviewed long ago (e.g. *Ibis* 107:552, 1965) so I will only mention its principal features here. Only British birds are covered; 320 species are illustrated in color by Donald Watson, whose paintings are first class. This is more than a field guide—the species accounts often run to 30 lines and are packed with information on life history. There are introductory sections on the classification of British birds, an introduction to the orders and families, special features of a birds' anatomy, flight, behavior, and breeding. Bruce Campbell's text is interesting, informative, and well-written. It is a pity that such an excellent book, in its reduction to pocket size, has developed the glaring flaw of miniscule print. A British

birder might still find it worthwhile to have this book in his pocket just for the plates, which are well reproduced and present a large enough image of the birds to provide a useful reference. American birders will want a more comprehensive European guide.

The Lippincott book was published in England by Collins and is the latest in the series of Collins field guides. Its appearance marks the debut of a young German artist, Hermann Heinzel, onto the stage of the world's bird painters—and I think he deserves a standing ovation. A field guide stands or falls on its illustrations, and there is little doubt that this one will stand. Color reproduction is good and the paintings are lifelike, accurate, and there are plenty of them. The wealth of illustrations is amazing, extending beyond the illustration pages onto the text, in margins, in the introduction, even into the table of contents where every family heading is accompanied by a miniature member of the family. Coverage is about the best I have ever seen; in addition to the usual flight pictures and immature plumages, most of the well-marked races are shown. There is a two-page spread of all wagtails of the *Motacilla flava* and *M. alba* complexes, for instance, and space is devoted to the races of the Jay, Coal Tit, Chaffinch, and others which exhibit considerable geographic variation within the area. Also pictured are some of the commoner escapes and introduced birds (chiefly anatids and phasianids) which frequently confuse the beginner who cannot find them in the average bird book. Another nice feature is the drawing of wing formulas for certain critical species pairs, such as the Reed and Marsh Warblers, and Willow Warbler and Chiffchaff.

Here and there a few soft spots appear—no artist is perfect; Mr. Heinzel needs more practice and probably more field experience with some groups to get the poses better. Shorebirds are one of his least successful groups; I would not have recognized the fat little bird on the rock on page 133 as the slim and dainty Common Sandpiper. He does not understand the soul of a cormorant—some of his are duck-like, while the flying Shag has a curiously-shaped neck, as if it were a plasticene model that someone had grasped with one hand while pulling the head with the other, stretching the neck thin. The Reef Heron has an unnatural-looking kink in its neck; it has been bent while remaining stiff, thus resembling a contorted pipe-cleaner. Its white-phase companion should not be perched in a tree, either. It is well that the Pied-billed Grebe is labelled—it might be anything. The Garden Warbler has turned out poorly; an all-brown bird should not have an olive-gray head and mantle. All this means only that Mr. Heinzel has flubbed a few lines—he has still put on a star performance, and I hope we will see many more paintings from his brush.

Richard Fitter is an experienced writer with many bird books to his credit, and he has done an outstanding job on the text. Tight, compact, without a line of padding, it complements the illustrations with additional field notes and descriptions of plumage, voice, and habitat. Unlike the Oxford book, this one is purely a field guide, and so contains nothing on life history. Although the text is businesslike and not discursive, Mr. Fitter still found room for an occasional light touch, as when he describes the flight outline of the Griffon Vulture as "like a teatray in the sky." Also, he notes that the Sacred Ibis is the emblem of the British Ornithologists' Union, which is presumably not intended to be a good field mark. Thanks to Mr. Fitter's efficient writing, the book is the same size as the standard European field guides even though it treats more species. This additional coverage has, however, necessitated the use of smaller print; while not unreadable, it is still hard on the eyes.

The format is that which has recently become popular for field guides—text and maps on the left-hand page, illustrations on the right. John Parslow has done an excellent job

on the maps, which in general remain clear and readable although prone to all the defects inherent in miniature size (one inch square). The maps of the Brown Booby and Red-billed Tropicbird appear blank at first glance, until one's trusty magnifying glass shows them to occur in the two little prongs of the Red Sea which just show on the lower edge of the map. These are exceptions; the colors (blue for winter range, green for resident, yellow for breeding) stand out fairly well from each other, although on narrow coastal strips it is hard to see the boundary between blue and green.

Discussion of maps brings me to perhaps the most important feature of the book—its range of coverage. The maps cover Europe, Iceland, Russia and the Middle East east to Long. 60° East, and North Africa south to Lat. 28° North. All the birds of North Africa and the Middle East are illustrated and covered as fully as the European birds; so whether you are hound for Morocco or the Atlas Mountains, Iceland, or Lebanon, this one book covers their birds. An attractive page of babblers from the deserts rubs shoulders with a page of vagrant thrushes from Siberia. This feature alone would make the book worth buying.

A reviewer is duty bound to find some faults, however good the book he is reviewing, and inevitably writers are kind enough to come up with some errors to make his job easier. The book has a few taxonomic curiosities—*Tachybaptus* for the genus of the Little Grebe and *Calonectris* for the genus of Cory's Shearwater. Bean Goose and Pink-footed Goose are treated as separate species, although they have been considered conspecific at least as far back as Delacour and Scott (1954. *The Waterfowl of the World*). "Bustards are placed between cranes and rails, a novel approach even in so controversial an order as the Gruiformes"—this is a direct quote from my review (*Wilson Bull.* 83: 449, 1971) of the "Hamlyn Guide to Birds of Britain and Europe," which adopted the same order; the error has here been repeated.

English names follow the standard practice of using no modifier for birds which are represented by only one member of a family or group in Britain, e.g. "the" Teal, "the" Swallow, etc. But in this guide horizons have broadened considerably. While "the" Wren may be admissible since there is no other wren in the region, I think "the" Wheatear is a bit unimaginative for *Oenanthe oenanthe* when no less than 12 other wheatears are covered by this book. On the other hand, "Andalusian Hemipode" as the name for the local *Turnix* is always good for a giggle—I'm glad they left it in.

The Bar-headed Goose is wrongly stated to be a native of India; it is a native of north-central Asia, visiting India only in the winter. No range is given for the Pied Stonechat, either as a map or in the text. The labels under the illustrations of the See-See Partridge and the Sand Partridge have been transposed. An odd typo has crept in to provide us with a little amusement—the immature Steppe Eagle is described as being "sometimes with white ump patch" (mature birds are presumably over the ump).

I find occasional exceptions to the generally very high quality of field identification notes. The best way to tell a Lesser Kestrel from a Kestrel is by the very pale, almost white underside to the wing; this is neither mentioned nor is either bird shown in flight from below. I would find it hard to tell the skuas (jaegers) apart by the clues given in this book; Arctic (Parasitic) is compared with Pomarine rather than with Long-tailed, while of the latter it is said: "immature distinguishable from other immature skuas by small size!! (exclamation marks mine), smaller bill (!!!) and much less white in wings." Sounds easy, doesn't it? Until you try it. Of the Shorelark (= Horned Lark, *Eremophila alpestris*) it is said: "Song recalls Skylark's but is briefer." If this is true, which I doubt, then the European bird must be a good species, since the song of our

Horned Lark bears no resemblance at all to that of a Skylark. Finally, the most striking character of Upcher's Warbler in the field is its habit of cocking its tail constantly. This has not been mentioned although it is the best way to tell Upcher's from Olivaceous Warbler, from which it is stated to be "hardly identifiable in field."

These are all small points. This remains a really excellent book, one that has earned itself a place in the field guide hall of fame. It comes with the additional bonus of a sturdy cloth binding, in contrast to certain recent guides. Artist, writer, and cartographer are all deserving of the highest praise. Even if you already own other European bird books, this one is a must for your collection.—STUART KEITH.

HAWAIIAN BIRDLIFE. By Andrew J. Berger. Univ. Press of Hawaii, Honolulu, 1972: 270 pp., maps, 123 photos, 59 col. pls. \$15.00.—This is a state bird book of a different and significant type. It thoroughly documents the ornithological history of the whole Hawaiian archipelago (all the way to Kure beyond Midway) and summarizes most of the studies and current knowledge of all Hawaiian birds whether native or introduced. It also takes repeated documented conservation stands for the preservation of native habitats and halting introduction of alien birds or mammals. The survival of many of the remaining fascinating birds endemic to Hawaii, mostly in the unique family Drepanididae, now hangs in the balance, with discouragingly little progress being made to assure their continued existence. It is to be hoped that Berger's book, giving the tragic history of the extinction of many Hawaiian species and the current plights of many survivors, will be a powerful force in helping save native Hawaiian birds.

The four chapters of the book are detailed treatments of: the habitats, habitat changes wrought by man, and evolution of Hawaiian birds; the indigenous species—namely breeding sea birds; the endemic species—chiefly the native land, marsh, or water birds; and the numerous introduced birds, except for gallinaceous species. In the last three of these chapters the Hawaiian literature on most species has been thoroughly covered, and often much information is given on breeding biology, behavior, adaptive physiology, and other subjects. The author's and his co-worker C. R. Eddinger's exciting first discoveries of nests and eggs of several endemic birds and their studies of the nestlings, some raised and even bred in captivity, are recounted rather fully. Some of the old authors, especially Perkins, from the turn of the century are quoted extensively in trying to give all that is known (and, too often, all that ever will be known) about the endemic birds. Appendices complete the thoroughness of the book in giving annotated lists of Hawaii's several hundred species of migrants and stragglers, as well as species introduced without known establishment. The bibliography of about 300 cited references will be especially valuable for anyone studying Hawaiian birds.

In spite of the overall excellence of Berger's book, even to near-perfect proofreading, some lesser adverse criticisms arise. The numerous photographs, although mostly of high quality, including the several remarkably fine ones taken by W. K. Fisher in 1902, include an inordinate number of pictures of nests, eggs, and nestlings. Some of these are notable "firsts" but many do not convey enough information to justify so much space. The numerous Hawaiian birds shown in twelve new paintings are, unfortunately, rather rough and unlikelike, although the detailed botanical backgrounds are fine. The paintings do not reflect the availability of many distinguished bird artists in this country, and they also stand in poor contrast to the seven, 80-year-old, masterly colored lithographs reproduced from Rothschild.

Vernacular names of Hawaiian birds are bound to lead to confusion and Berger has met some of the problems by using some subspecific common names or by including (but not consistently enough) Hawaiian language names. Newell's Shearwater (*Puffinus puffinus newelli*), for instance, is not given its Hawaiian name nor acknowledged as a race of Manx Shearwater. Some confusion also results in the attempted major separation of indigenous and endemic birds, with the endemic races of Dark-rumped Petrel and Manx Shearwater put in the indigenous section, but endemic races of other wide-ranging species (Short-eared Owl, Black-necked Stilt, etc.) grouped with endemics. Curiously, too, the introduced Jungle Fowl is put under endemic birds!

Adverse comments notwithstanding, "Hawaiian Birdlife" is an important book, very reasonably priced, and a rich source of information and pleasure. There is no other book to compare with it.—FRANK RICHARDSON.

THE WORLD OF THE WILD TURKEY. By James C. Lewis. J. B. Lippincott Co. Philadelphia, 1973: 158 pp., photos. \$5.95.—Another book on the Wild Turkey might seem premature with such works still available as Hewitt (*The Wild Turkey and its Management*, The Wildlife Soc., 1967) and Schorger (*The Wild Turkey, Its History and Domestication*, Univ. Okla. Press, 1968). Roger Latham's *A Complete Book of the Wild Turkey* (Stackpole, 1956), long the only good book available, is now out of print.

James C. Lewis's book is well written and beautifully illustrated, filling the niche left by Latham. He has included much of the new information obtained through better means of capture and radio-tracking. The Wild Turkey is one of seven birds, 20 mammals, and four other animals so far treated in Lippincott's Living World series, which explores "the living world of these animals." This biography is excellently suited for high school students or general readers. Lewis's selection of photographs is good, but unfortunately some are poorly reproduced, such as the strutting tom (p. 36) which is used to much better advantage on the glossy dust cover. If the bird shown on page 50 is a Common Raven, the picture would have been best left out, the bird being more crow-like than raven-like.

The book is accurate on the whole, but suffers from several errors and lapses. The northeastern populations of turkeys from West Virginia, Pennsylvania, and New York receive little attention while perhaps too much attention is given to Missouri and Florida birds. Lewis repeats Schorger's mistaken idea that the beard is intermediate between filoplumes and contour feathers; Lucas and Stettenheim (*Agr. Handbook* 362, 1972) have shown that these structures are not feathers but solid horny fibers. In giving weights (p. 28), the author seems to juggle numbers with average weights of hens—9.2 pounds for West Virginia hens as compared with 11.5 pounds for Missouri hens, yet he doesn't indicate what time of year his samples were taken. Further on, he rightly states that there is a 15% variation in weight throughout the year.

The freeze position of the poult is nowhere well described or illustrated. In truly wild birds, poults will, on signal from the hen, crouch flat and extend the head and neck and remain thus until released by another call from the hen. Poults can be picked up in this position, toe punched, and returned to the ground without changing their position. I can't believe what is currently accepted by many, that the Great Horned Owl "is the most effective night predator." I have never read a description of an actual attack by an owl on a Wild Turkey, and it seems to me that owl feathers near the kill, or bones or feath-

ers of poults in pellets would be better evidence than "talon marks on neck and base of wings." An account Lewis repeats of two Golden Eagles cooperating in an attack on turkeys could be counterbalanced by an account in Texas of two hens cooperating in driving off an attacking Zone-tailed Hawk (Johnson, *Auk*, 78:646, 1961).

Lewis reports that "Most states with gobbler-only hunting laws consider a bearded hen legal game, because hunters rely heavily on the beard to identify gobblers, especially in the fall." This statement may be partially true but it deserves comment. With a tom approaching, who looks for a beard? Turkeys are mad or sexually aroused depending on the season, so in hunting, the best character for sexing a turkey is behavior, then color, then size, and finally the beard. In our studies of New York turkeys, nine percent of 98 hens banded in the fall were bearded, so they would have been legal game in the spring gobbler hunt. This mistake in management should be corrected rapidly as there is little need to use the beard in sexing turkeys, and a hen, particularly in the spring, is an important member of the turkey world.

I recommend this book highly to advanced high school students, college students, and to any general readers interested in being introduced to our uniquely North American bird.—STEPHEN W. EATON.

LES OISEAUX DU QUÉBEC. By Raymond Cayouette and Jean-Luc Grondin. La Société zoologique de Québec, Inc., Orsainville, Québec, 1972; paper covered, 117 pp., many drawings. Price not given.—This book on birds of the Province of Quebec is intended to supplement field guides for identification, and is not a scientific treatise for skilled ornithologists. Grondin, an artist, has illustrated some 243 of the 350 bird species of the province. His beautiful black-and-white drawings are both artistic and accurate in portraying the shape, silhouette, proportions, and morphological features of each species. The species have been mostly arranged in taxonomic order, but the sequence has been altered in some cases for the sake of the artistic presentation of the drawings.

Compared to Godfrey's *Les Oiseaux du Canada* (Natl. Mus. Canada, Bull. 203, 1967) and *Encyclopédie des oiseaux du Québec* (Editions de l'Homme, Montréal, 1972), the present book is a more popular work. The authors concisely treat the general life history of each species, habitats, vocalizations, migration, wintering grounds, and breeding range in Quebec. The appearance of each species is described briefly, but only insofar as is necessary to complement its illustration. The illustrations do not show colors nor the plumage variations according to sexes and age; except where otherwise indicated, the drawings represent males in spring feather.

Three indexes conclude the book; the first gives the French name of each species, followed by English and scientific names; the second gives English names followed by corresponding French names; and the third one lists some 175 vernacular or folkloric names.

This book will appeal to nature lovers, particularly those interested in a better knowledge of birds, if for nothing more than its beautiful drawings.—RAYMOND McNEIL.

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Parodi's Tanager, *Hemispingus parodii*, a new species from Peru.
Painting by John P. O'Neill.

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HEMISPINGUS PARODII, A NEW SPECIES OF TANAGER FROM PERU

JOHN S. WESKE AND JOHN W. TERBORGH

In the course of field work on the ecology and distribution of birds in the eastern Andes of Peru, we encountered a tanager that appears to represent a new species, as described below (and see frontispiece).

Hemispingus parodii sp. nov.

PARODI'S TANAGER

HOLOTYPE.—American Museum of Natural History No. 810,463; Adult male from the Cordillera Vilcabamba, 12°36'S, 73°29'W, elevation 3,480 m. Dept. of Cuzco, Peru; 28 July 1968; collected by John S. Weske and John W. Terborgh; prepared by Weske; original No. 1849.

DIAGNOSIS.—A moderately large *Hemispingus*, nearest *H. calophrys* (Sclater and Salvin, 1876) of the Bolivian Yungas but throat yellow; superciliary stripe yellow and decidedly narrower; crown, lores, and face patch dusky olive; nuchal area with a less pronounced demarcation in color between crown and back; back slightly darker greenish olive; and abdomen more yellowish.

DISTRIBUTION.—At elevations from about 3,200 to 3,500 m on the crest and upper slopes of the northern Cordillera Vilcabamba in the Province of La Convención, Department of Cuzco, Peru. The type locality lies on a high ridge bordering the canyon of the Río Mapitunari, a tributary of the Río Apurímac.

DESCRIPTION OF THE HOLOTYPE.—Back, rump, and upper tail coverts between Citrine and Dark Citrine (capitalized colors are from Ridgway, 1912); crown dusky olive, darker on forehead and lighter posteriorly, the individual feathers being dull blackish with Dark Citrine edgings and basal areas; chin and throat Lemon Chrome; malar area and anterior breast between Lemon Chrome and Primuline Yellow; flanks and sides of breast Citrine; central breast and belly near Lemon Chrome but slightly duller; under tail coverts Sulphine Yellow. A Lemon Chrome superciliary stripe from the base of the bill to the nape, brightest over the eye, the individual feathers being finely tipped with olive; lores and postocular region olive; auriculars and suboculars dull yellowish with paler shaft streaks; postauricular patch Dark Citrine, bordered posteriorly by a dull yellowish streak extending from the throat. Remiges dusky; primaries edged with Sulphine Yellow; secondaries, tertials, and upper wing coverts with margins the color of the back; rectrices with Dark Citrine outer webs and dusky inner webs; tail moderately

graduated, the outermost rectrices being ca. 11 mm shorter than the central (and longest) ones. Soft part colors (in life): maxilla black; mandible medium gray; tarsi and toes pale gray; and iris dark brown.

MEASUREMENTS OF THE HOLOTYPE (mm).—Chord of wing 72.7; tail (from insertion of the two central rectrices to the tip of the longest rectrix) 69.9; tarsus 22.4; bill length (from anterior edge of nostril to tip of maxilla) 7.8; bill depth (at posterior edge of the nostril) 4.9.

ETYMOLOGY.—It is a pleasure to name this species in honor of our friend José Parodi Vargas, who provided us with a base for our expeditions at his Hacienda Luisiana and generously aided us in countless other ways.

REMARKS

Variation in the Type Series.—The eight specimens at hand vary individually in darkness of crown pigmentation but otherwise are quite uniform. One male is blackish on the forecrown and dusky on the occiput, while at the other extreme, another male has a dusky forecrown and a hindcrown which is mainly olive and only slightly darker than the back. On one female, the dusky centers of the crown feathers form fairly distinct streaks, but in the other the crown appears unstreaked and closely matches that of the holotype. Females average smaller than males but otherwise are externally indistinguishable. There is no significant variation in soft part colors.

Habitat.—The habitat of *Hemispingus parodii* is a mixture of elfin forest and tall grassland on the uppermost slopes of the northern Cordillera Vilcabamba. Treeline is ill-defined in this area, but with increasing elevation there is progressively more grassy vegetation and a reduced number of woody plants. Trees are short and gnarled, with a profuse epiphytic covering including lichens, orchids, and bromeliads. Several kinds of bamboo and one species of tree fern are found also. The area is one of cool temperatures and high humidity, for the slopes are customarily in the clouds by day except in early morning. We found *H. parodii* from the summit of the range at 3,520 m down to an elevation of 3,190 m. The general habitat is the same as that of *Gallinago imperialis* and was pictured by Terborgh and Weske (1972).

Breeding Information.—Data on the gonadal condition in our series of *H. parodii* provide a basis for tentatively determining the species' breeding season. Two males taken in early August were in full breeding condition, each having 10 mm testes and a cloacal protuberance (1 and 5 August). The testes of four males collected in mid and late July were considerably enlarged (15 July—6 mm testes; 15 July—9 mm; 21 July—9 × 5 mm; 28 July—left testis 9 × 5 mm and right, 7 × 5 mm). None of these birds had a cloacal protuberance. A female taken 24 July was in breeding condition (ovary and oviduct much enlarged, largest ovum 6 mm) but two August birds were not (2 August—ovary 4 mm, not enlarged; 10 August—ovary 5 mm, largest ovum 1½ mm). These data suggest that the breeding season

for *H. parodi* was just beginning in late July. That breeding had not occurred earlier is suggested by the absence of any juvenal birds or birds with incompletely pneumatized skulls, by the lack of females with a brood patch, and by the relatively unworn plumage of our specimens. Unfortunately we have no information on vocalizations or other behavior.

Ecological Relationships.—A feature of avian distribution on the slopes of the Cordillera Vilcabamba is elevational replacement of ecologically similar species. In accordance with the competitive exclusion principle, evidence points to competition between congeners as a mechanism limiting their respective elevational ranges (Terborgh, 1971). In the northern Cordillera Vilcabamba, *Hemispingus parodii* appears to replace the species *H. atropileus* in the highest montane regions. *H. atropileus*, a slightly larger bird, is common in elfin forest from 2,600 to 2,800 m and was found once at 3,300 m, above the lower elevational limit of *parodii* and in the same netline in which several *parodii* were caught. On the west side of the Apurímac Valley, where *parodii* is not present, *atropileus* ranges to the upper limit of trees. Seemingly, it has been able to expand its elevational range in the absence of competition from its congener. Two much smaller congeneric species, *H. superciliaris* and *H. xanthophthalmus*, have elevational ranges which overlap those of *parodii* and *atropileus* in the Cordillera Vilcabamba, but we feel that they are sufficiently different in size and feeding behavior to minimize competition with the latter two.

All individuals of *H. parodii* that we encountered were trapped in mist-nets. Birds of this species comprised 1.3 percent of our captures in nets from 3,170 to 3,340 m elevation and 0.5 percent of the catch at 3,500 m. Based on capture rates, the commonest species in the area were the tanagers *Iridosornis reinhardti* and *Anisognathus igniventris*, the hummingbird *Metallura tyrianthina*, the flower-piercer *Diglossa lafresnayii*, the finch *Catamenia homochroa*, the furnariid *Schizoeaca fuliginosa*, and the flycatcher *Ochthoeca frontalis*.

Another fairly common species at these elevations is *Basileuterus luteoviridis*. This large warbler bears a striking similarity to *Hemispingus parodii* in color and size. The two species are alike in having citrine upperparts, yellow underparts and superciliaries, and olive facial markings. They are most readily distinguished by crown color—citrine, like the back, in *B. luteoviridis* but dusky olive in *H. parodii*. In addition, *B. luteoviridis* has flesh-colored tarsi and toes, longer rectal bristles, and a flatter bill with a solid black mandible. *B. luteoviridis* is a bird of dense cloud forest understory as well as elfin forest. In the Cordillera Vilcabamba its elevational range is much broader than that of *H. parodii*, extending from 2,100 m to 3,520 m.

TABLE 1
MEASUREMENTS IN MILLIMETERS OF THREE SPECIES OF *HEMISPINGUS*

| Measurement | <i>H. parodii</i> | | | | <i>H. calophrys</i> | | | | <i>H. atropileus auricularis</i> | | | |
|-------------|-------------------|------|------|-----------|---------------------|------|------|-----------|----------------------------------|------|------|-----------|
| | N | Mean | S.D. | Range | N | Mean | S.D. | Range | N | Mean | S.D. | Range |
| MALES | | | | | | | | | | | | |
| Wing chord | 6 | 72.0 | 0.9 | 70.8-73.0 | 7 | 70.0 | 3.4 | 65.8-73.9 | 15 | 75.6 | 3.5 | 70.1-80.4 |
| Tail length | 6 | 68.4 | 1.4 | 66.0-69.9 | 7 | 66.8 | 2.0 | 63.3-69.2 | 15 | 72.5 | 3.0 | 67.3-79.0 |
| Bill length | 6 | 7.8 | 0.2 | 7.5-8.1 | 7 | 7.7 | 0.4 | 7.2-8.4 | 14 | 8.7 | 0.3 | 8.0-9.2 |
| Bill depth | 6 | 4.8 | 0.2 | 4.5-5.1 | 5 | 5.0 | 0.2 | 4.8-5.3 | 14 | 5.5 | 0.2 | 5.0-5.7 |
| FEMALES | | | | | | | | | | | | |
| Wing chord | 2 | 69.0 | — | 67.5-70.5 | 4 | 67.4 | 2.4 | 64.4-70.1 | 10 | 72.9 | 4.2 | 65.1-80.5 |
| Tail length | 2 | 66.4 | — | 65.8-66.9 | 4 | 65.6 | 1.8 | 63.1-66.9 | 9 | 71.4 | 3.6 | 65.2-77.9 |
| Bill length | 2 | 8.2 | — | 8.0-8.3 | 3 | 7.6 | — | 7.0-7.9 | 10 | 8.7 | 0.2 | 8.5-9.0 |
| Bill depth | 2 | 5.1 | — | 4.8-5.3 | 3 | 4.9 | — | 4.9-5.0 | 9 | 5.4 | 0.2 | 5.2-5.7 |

Symbols: N—sample size, S.D.—standard deviation.

The significance, if any, of the apparent convergence in the two species is not evident.

Systematic Relationships.—In investigating the systematic relationship of *Hemispingus parodii*, we have been led to review the status of the races of *H. atropileus*, which shows considerable resemblance to the new form. Hellmayr (1936) considered *H. atropileus* to consist of three or possibly four subspecies: nominate *atropileus* of eastern Colombia and Ecuador; *chlorigaster*, a western Colombian race perhaps not distinct from *atropileus*; *auricularis*, a somewhat smaller Peruvian form with brighter underparts but like the nominate race in having a narrow, whitish superciliary line; and *calophrys* of Bolivia, a still smaller form with a broad, golden ochraceous superciliary. The race *intermedius*, described by Carriker (1931) from northern Peru, was considered by Zimmer (1947) to be indistinguishable from *auricularis*. It is clear that *H. parodii* and *H. atropileus auricularis* are not conspecific, since their ranges meet and overlap slightly, as was shown above, and there is no indication of intergradation. Since *parodii* and *calophrys* are allopatric, the possibility exists that they are conspecific. Such a taxonomic arrangement would entail recognition of *calophrys* as a species distinct from *H. atropileus*. The habitat, climatic, and elevational preference of *calophrys* is apparently similar to that of *auricularis* and *parodii*. Elevations noted on *calophrys* specimen labels are 3,500 m, 10,000 ft, and 10,700 ft. Bond and Meyer de Schauensee (1942) describe two of its localities with terms like "cold, foggy, and rainy" and "forest and boggy meadows." We have been able to locate only 16 specimens of *calophrys*, all from the Yungas

TABLE 2

COMPARISON OF PLUMAGE COLORATION AND PATTERN IN THREE SPECIES OF *HEMISPINGUS*

| Character | <i>H. parodii</i> | <i>H. calophrys</i> | <i>H. atropileatus auricularis</i> |
|---------------------------------|--------------------------|---------------------|------------------------------------|
| Crown patch | | | |
| Width | Wide | Narrow | Wide |
| Color | Dusky olive | Black | Black |
| Superciliary stripe | | | |
| Width | Narrow | Wide | Narrow |
| Color | Yellow | Orange-ochraceous | White or buffy-white |
| Face patch | | | |
| Width | Narrow | Narrow | Wide |
| Color | Dark olive | Blackish to dusky | Black |
| Throat color | Yellow | Orange-ochraceous | Ochraceous yellow |
| Color of central abdominal area | Yellow tinged with olive | Yellowish olive | Yellow tinged with olive |

of Bolivia in the Departments of La Paz and Cochabamba. We have examined all of these except the holotype, from Tilo Tilo and now in the British Museum, and two individuals, one from Sandillani and one from the La Paz vicinity, now in Munich. No information on the biology of *calophrys* is available in the literature to aid in determining its taxonomic status.

The range of *parodii* and the nearest locality for *calophrys*, not far northeast of La Paz, lie about 750 km apart. The intervening area of Andean slope in southeastern Peru has been visited by such collectors as Chapman, Watkins, and Carriker, but no specimens resembling either of the two forms have been taken. The richness of the black and golden-ochre head coloration varies within the series of *calophrys* specimens at hand, but no morphological trend toward *parodii* in specimens from geographically nearer localities is apparent. Similarly, there is a gap of 570 km between the southernmost locality for *H. atropileus auricularis* (Occobamba Valley, Depto. Cuzco) and the nearest point in the range of *calophrys*. Measurements and characteristics of *parodii*, *calophrys*, and *auricularis* are summarized in Tables 1 and 2. *H. calophrys* seems to differ about equally from *H. parodii* and *H. atropileus auricularis* in plumage coloration and markings. In size, it is similar to the former and somewhat smaller than the latter. Until additional information is available on vocalizations of the various forms and on populations in geographically intermediate areas, if any, it seems best to consider *H.*

parodii and *H. calophrys* each as full species and to recognize *H. atropileus* as a polytypic species (comprising populations to which have been applied the names *chorigaster*, *intermedius*, *auricularis*, as well as *atropileus*), ranging from Colombia to Peru near the city of Cuzco.

SPECIMENS EXAMINED

The museums housing the specimens are cited in parentheses: AMNH, American Museum of Natural History; USNM, U.S. National Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; NS, Naturmuseum Senckenberg; LSU, Louisiana State University Museum of Zoology; FM, Field Museum of Natural History.

Hemispingus parodii.—PERU: Cordillera Vilcabamba (all from within 2 km of the type locality), 6 ♂♂, 2 ♀♀, 1 ♀ skeleton (AMNH), 1 unsexed alcoholic (USNM).

Hemispingus calophrys.—BOLIVIA: Hichuloma, 1 ♂, 1 ♀ (ANSP); Incachaca, 1 ♂ (ANSP); Cillutincara, 1 unsexed (AMNH); Unduavi, 1 ♂, 1 ♀ (NS); Km 104, Prov. Chapare, 4 ♂♂, 2 ♀♀, 1 unsexed (LSU).

Hemispingus atropileus auricularis.—PERU: Cordillera Vilcabamba, 2 ♂♂, 2 ♀♀ (AMNH); Puncu, Depto. Ayacucho, 1 ♂ (AMNH); Yuraceyacu, Depto. Ayacucho, 2 ♀♀ (LSU); Tocopoqueu, Occobamba Valley, 1 ♂ (AMNH), 1 ♂ (USNM); Maraynioc, 2 ♂♂, 1 ♀ (AMNH), 1 ♂ (USNM); Rumicruz, 1 ♂, 2 unsexed (AMNH); Cordillera Carpish, 3 ♂♂, 1 ♀, 1 unsexed (LSU); Carpish Pass, 1 ♀ (AMNH); Carpish Ridge, 1 ♂, 1 ♀ (FM); Bosque Zapatagocha, Depto. Huánuco, 1 ♂ (FM); La Lejia, 1 ♂, 2 ♀♀ (AMNH).

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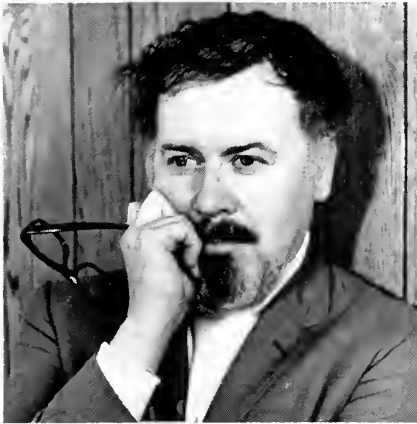
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BIRD AND MAMMAL LABORATORIES, BUREAU OF SPORT FISHERIES AND WILDLIFE, NATIONAL MUSEUM OF NATURAL HISTORY, WASHINGTON, D.C. 20560, AND DEPARTMENT OF BIOLOGY, PRINCETON UNIVERSITY, PRINCETON, NEW JERSEY 08540. ACCEPTED 28 JANUARY 1974.

NEW LIFE MEMBER



Donald Richard Eckelberry is now a Life Member of the Wilson Ornithological Society. He was born in Sebring, Ohio, and at an early age developed a love of nature and later a facility for painting it. He studied at the Cleveland Institute of Art, and after he left there he pursued a number of jobs before becoming a premier artist and illustrator of birds. He has travelled widely in pursuit of birds, for he prefers to paint species that he knows. Among his best-known feats of illustration are those in Richard Pough's *Audubon Bird Guides* and James Bond's *Guide to the Birds of the West Indies*. Mr. Eckelberry has written several articles on nature and is a member of various organizations, including the A.O.U. He is married and lives in Babylon, Long Island, New York.

FOOT-SCUTE DIFFERENCES AMONG CERTAIN NORTH AMERICAN OSCINES

GEORGE A. CLARK, JR.

Although avian species often differ in arrangement of the scutes and papillae of the feet (Blaszyk, 1935; Staaland, 1964; Morlion, 1968; Clark, 1972, 1973a), the extent of differences remains undescribed for most birds. I here report selected examples of such differences among North American oscine species and suggest some initial interpretations. The species discussed were chosen in view of their potential interest for functional or systematic interpretation.

MATERIALS AND METHODS

I have examined more than 6000 study skins of 250 North American oscine species, using a binocular dissecting microscope or hand lens to study foot scutellation. Specimens were at the University of Arizona, Harvard Museum of Comparative Zoology, Yale Peabody Museum of Natural History, U.S. National Museum of Natural History, and the University of Connecticut. Throughout the text, a statistically significant difference refers to a probability of less than 0.01 in a Chi-square test. As I have found no evidence for a statistically significant bias between right and left feet within a species, I inspected only the right foot for most species.

OBSERVATIONS AND PRELIMINARY INTERPRETATIONS

Verdin (*Auriparus flaviceps*).—Although usually placed among the Paridae, the Verdin differs sufficiently from typical parids to suggest to Taylor (1970) the possibility of a coerebid affinity. Among Verdins that I have examined ($n = 25$), 64 percent have an intact scute in a position equivalent to that found at the base of the two outer toes in thrashers (*Toxostoma*; Clark, 1972: Fig. 2). In contrast, parids (*Psaltriparus*, *Parus* spp.) and coerebids (*Coereba*, *Cyanerpes*, *Conirostrum*) that I examined typically have a divided scute in this position. In addition, coerebids as a rule have nine scutes in the row along toe II, whereas small parids commonly have fewer (seven in *Auriparus*). Thus in this regard the Verdin is like Paridae rather than Coerebidae, but it differs from both in the high incidence of an undivided basal scute.

Wrentit (*Chamaea fasciata*).—The affinities of the Wrentit have been a controversial subject, but many authorities believe it to be related to the Timaliidae (Mayr and Short, 1970). Species of North American Cinclidae, Troglodytidae, Mimidae, and Turdidae, to which *Chamaea* might be related, have two narrow scutes adjacent to one another at the proximal end of toe IV near its confluence with toe III (Fig. 1). These two narrow scutes are absent in the Wrentit, which is thus like many genera of Old World Timaliidae.

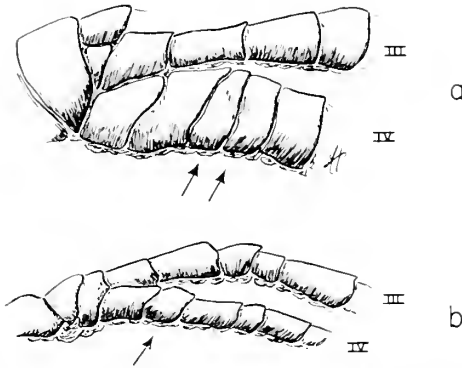


FIG. 1. a) Two narrow scutes near the base of toe IV in a typical thrush (Eastern Bluebird, *Sialia sialis*); b) only one such scute in a typical parulid (Ovenbird, *Seiurus aurocapillus*).

Wrens (*Thryothorus*).—In this genus, two Mexican species for which Grant (1966a) found no notable difference in habitat utilization differ significantly in scutellation. The Happy Wren (*T. felix*; $n = 10$) has an intact scute at the proximal end of rows extending along the dorsal surface of toes III and IV, in contrast to a divided scute in the corresponding position in the Bar-vented Wren (*T. sinaloa*; $n = 20$). All ten species of wrens occurring in the United States are like the Bar-vented Wren. I have no explanation for the departure from "normal" in *T. felix*, but the case does illustrate the divergence that can occur in closely related species.

Kinglets (*Regulus*).—Golden-crowned Kinglets (*R. satrapa*; $n = 16$) differ from Ruby-crowned Kinglets (*R. calendula*; $n = 26$; Fig. 2) in having one more scute near the distal end of toe IV. Grant (1966b) observed more hanging during feeding by Golden-crowns than by Ruby-crowns; conceivably the extra scute on the outer toe of the Golden-crowns might aid in this behavior by allowing greater bending. In the past, *R. calendula* has been placed in a separate genus, *Corthylio*.

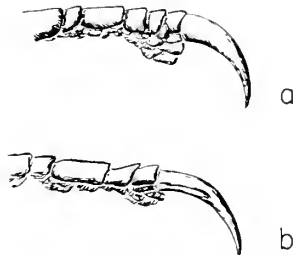


FIG. 2. Distal end of toe IV: a) Golden-crowned Kinglet with three scutes adjacent to claw; b) Ruby-crowned Kinglet with two scutes adjacent to claw.

Olive Warbler (*Peucedramus taeniatus*).—Although the Olive Warbler has generally been considered a parulid, George (1962, 1968) has emphasized its aberrant features and removed it from that family. In scutellation I find that *Peucedramus* differs from parulids (e.g., *Vermivora*, *Parula*, *Dendroica*, and *Wilsonia*) in having an extra scute at the proximal end of the rows of scutes extending along both toes III and IV. I have failed to find a *Peucedramus*-like condition in other families thus far examined, including the Muscicapidae (sensu lato) to which George (1962) thought it related.

Yellow-breasted Chat (*Icteria virens*).—This species, ordinarily placed among the Parulidae, is aberrant in numerous ways (Eisenmann, 1962a; Ficken and Ficken, 1962). *Icteria* also differs from all other examined parulids (including *Granatellus*) in scutellation, in possessing an intact scute at the confluence of toes III and IV and in having an extra scute on the second phalanx of toe III. In scutellation *Icteria* is unlike any other oscine examined.

Meadowlarks (*Sturnella*).—The Icteridae are a large and diverse group, and meadowlarks are seemingly bona fide members of the family. However, both Eastern (*S. magna*) and Western (*S. neglecta*) Meadowlarks typically have only two small scutes near the distal end of toe IV, in contrast to three such scutes in representatives of other North American icterid genera.

Rose-breasted Thrush-tanager (*Rhodinocichla rosea*).—This species is now generally placed among the New World nine-primaried oscine assemblage (Eisenmann, 1962b), but it forages like a mimid or thrush. I find that, unlike North American mimids or turdids (Fig. 1), *Rhodinocichla* lacks the two narrow scutes adjacent to one another at the base of toe IV. In this it agrees with the Thraupidae and allies.

Cardinal grosbeaks (*Cardinalis*).—Cardinals (*C. cardinalis*) and Pyrrhuloxias (*Pyrrhuloxia sinuata*) are frequently treated as congeneric (Gould, 1961; Bock, 1964), but they differ in scutellation patterns to a degree. Pyrrhuloxias ($n = 24$) have a divided scute at the base of toes III and IV, a condition typical of cardinaline finches, including the Cardinal (Clark, 1972; this study). However, 39 percent of sampled Cardinals ($n = 138$) had an intact scute at the base of toes III and IV; the difference is statistically significant. The variation in scutellation in Cardinals shows no simple age, sexual, or geographic association in my sample. While the two conditions of scutellation in Cardinals might be associated with an undetected behavioral dimorphism, perhaps more likely the variation is functionally unimportant with respect to use of the feet.

Towhees (*Pipilo*).—Brown (*P. fuscus*) and Abert's (*P. aberti*) Towhees are closely related emberizines that coexist in a limited area of southern Arizona: there their habitat utilization appears to be similar (Marshall, 1960). Among Brown Towhees ($n = 58$) I found that 21 percent had an

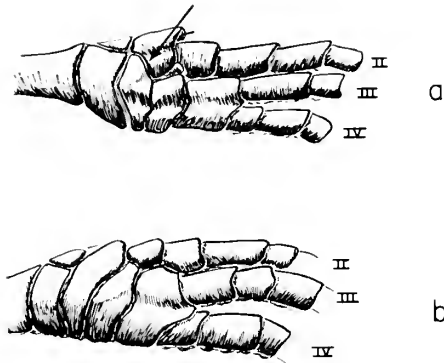


FIG. 3. Dorsal view of the base of the toes showing a) the divided transverse scute of a Fox Sparrow and b) the intact one of a Song Sparrow.

extra (third) scute near the distal end of toe IV. In contrast, 96 percent of Abert's Towhees ($n = 30$) possessed this scute. This statistically significant difference is structurally analogous to that between the kinglets. Green-tailed (*Chlorura chlorura*) and Rufous-sided Towhees (*P. erythrophthalmus*) resemble Brown Towhees in scutellation.

Sparrows (*Passerella* and *Melospiza*).—The Fox (*P. iliaca*) and Song (*M. melodia*) Sparrows are often considered congeneric (Mayr and Short, 1970). However, I find that the two differ in the condition of an elongate scute that lies transversely across the foot at the base of the toes (Fig. 3). In 98 percent of Song Sparrows ($n = 133$) the elongate scute was intact, but it was divided in 88 percent of Fox Sparrows ($n = 50$). The difference is statistically significant. Large Song Sparrows (*M. m. sanaka*) from the Aleutians, comparable to Fox Sparrows in body size, have the intact elongate scute typical for Song Sparrows of smaller body size. The Fox Sparrow is unique among examined emberizines in its divided scute; this is presumably a derived rather than primitive character among emberizines.

DISCUSSION

Only conjectural interpretations, if any, have been offered concerning the functional significance of the species differences found in this study. Similarly, Blaszyk (1935) was generally unable to provide a functional explanation for variations in passerine tarsal scutellation. However, he, Staaland (1964), and Lennerstedt (1972) did find partial association between the structure of toe pads and the size and nature of commonly used perches in European passerine species. Moreover, Clark (1973a) found notches in the toe pads of a number of only distantly related taxa of oscines that climb on trees or rocks. Detailed functional and behavioral studies seem necessary to

develop more precise ideas on the adaptive aspects of scutellation. Existing analyses of scutellation in reptiles (e.g., Horton, 1972; Kerfoot, 1970; Marx and Rabb, 1970) indicate that functional interpretation can be difficult due to complex interactions of genetic, developmental, physiological, and environmental factors.

The findings of this study and those of Clark (1972) indicate that significant differences in number of foot-scutes occur between species that are reasonably assigned to the Sittidae, Troglodytidae, Mimidae, Regulidae, Icteridae, Cardinalinae, and Emberizinae. However, unusual features of scutellation also occur in a number of genera aberrant in their respective families, e.g., *Auriparus* ("Paridae") and *Peucedramus* and *Icteria* (both "Parulidae"). Arrangement of foot-scutes might suggest new ideas on evolutionary affinities, but studies of scutellation of oscines from outside North America are needed to enable extended analysis. Caution must be used in interpreting the evidence of scutellation, for convergence and parallelism have probably occurred frequently (Clark, 1973b). As one example from the present study, the number of scutes near the distal end of the outer toe shows convergence between kinglets, icterids, and towhees.

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SUMMARY

This study provides new examples of taxonomic variation in foot-scutes. Coexisting, closely related, species sometimes differ significantly in the arrangement of foot-scutes; examples are *Thryothorus sinaloa*—*T. felix*, *Regulus satrapa*—*R. calendula*, *Cardinalis cardinalis*—*Pyrrhuloxia sinuata*, *Pipilo juscus*—*P. aberti*, and *Passerella iliaca*—*Melospiza melodia*. Variations in scutellation in some cases possibly correlate with behavioral differences, but marked variation within *Cardinalis cardinalis* might be functionally unimportant with respect to use of the feet.

Auriparus, *Peucedramus*, and *Icteria* are distinct in scutellation with respect to the families to which they are currently assigned, at least in North America. *Sturnella*, on the other hand, seems well-placed in the Icteridae, although it differs in scutellation from other North American members of the family. *Chamaea* is like many Old World Timaliidae in lacking two narrow scutes at the proximal end of the outer toe, as found in North American representatives of the Cinclidae, Troglodytidae, Mimidae, and Turdidae to which Wrentits have sometimes been linked taxonomically. The scutellation of *Rhodinocichla* resembles that of the New World nine-primaryed oscine assemblage more than that of mimids or turdids, to which relationship has also been suggested. Certain taxonomic interpretations of scutellation are tempting, but without more study

of function and of a wider array of species, this must be done with caution, particularly in view of variation between more clearly related taxa.

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TANTALUS MILNEEDWARDSII SHUFELDT—A SYNONYM OF
THE MIOCENE PHEASANT *MIOPHASIANUS ALTUS*
(MILNE-EDWARDS)

STORRS L. OLSON

Tantalus milneedwardsii, a supposed species of fossil stork, was named from a tibiotarsus from the Upper Miocene (Tortonian) deposits at La Grive-Saint-Alban, Département Isère, France, by R. W. Shufeldt ("1896" = 1897). When I encountered the type element of *T. milneedwardsii* in the National Museum collections, its non-ciconiiform appearance immediately aroused me to investigate its correct placement, particularly as Shufeldt is known to have committed many errors in identifying fossils. Comparison of the specimen with a series of modern avian tibiotarsi revealed that it is from a large galliform that ultimately proves to be referable to the species *Miophasianus altus* (Milne-Edwards).

TAXONOMIC HISTORY

The type and only specimen of *Tantalus milneedwardsii* is the proximal end of a right tibiotarsus (USNM 2168) of which Shufeldt (1897:513) said: "it was a *Tantalus* of almost precisely the same size as *T. loculator* [= *Mycteria americana*], and its tibio-tarsus presents characters agreeing very closely with that species. The agreement is so close that it would appear unnecessary to remove it from that genus. . . ." This nebulous statement, plus a single line drawing, is all that constitutes the original "description" of the species. Subsequently, the species has been listed variously as: *Tantalus Milne-Edwardsi* (Lambrecht, "1917" = 1918; 1921); *Pseudotantalus milne-edwardsi* (Sharpe, 1899); *Pseudotantalus Milne-Edwardsi* (Paris, 1912; Lambrecht, 1933); *Pseudotantalus Milne Edwardsi* (Ennouchi, 1930); and *Ibis milne-edwardsi* (Brodkorb, 1963). (Modern rules of nomenclature unfortunately require deletion of the hyphen.)

COMPARISONS AND DISCUSSION

In my comparisons of the type of *Tantalus milneedwardsii*, I find that it differs from storks and agrees with Galliformes in the broader and more oval shaft, the more expanded proximal end (Fig. 1a, b), the greater lateral projection of the much heavier outer cnemial crest (Fig. 1a, b), the more lateral displacement of the inner cnemial crest and the intermuscular line descending from it (Fig. 1a), and the presence of a well-developed, longitudinal nutrient foramen posterior to the distal end of the fibular crest (Fig. 1b, c). In proximal view (Fig. 1e) it differs vastly from the storks, in which



FIG. 1. Holotype tibiotarsus (USNM 2168) of *Tantalus milneedwardsii* Shufeldt = *Miophasianus altus* (Milne-Edwards). a, anterior view (the large chip from the end of the shaft had not been replaced at the time Shufeldt illustrated this specimen). b, posterior view. c, lateral view. d, medial view. e, proximal view. All figures $\frac{2}{3}$ natural size.

the cnemial crests are distinctly separated from the articular surfaces by a somewhat constricted pedicel. The fossil is clearly galliform and more particularly, a phasianid (*sensu lato*).

The deposits at Grive-Saint-Alban have produced ten named species of Galliformes, as well as other avian fossils. As given in Brodkorb (1964) the Galliformes are: *Palaeoperdix edwardsi* (Depéret), *Miophasianus medius* (Milne-Edwards), *M. altus* (Milne-Edwards), *M. maximus* (Lydekker), *Proalektor miocaenus* (Gaillard), *P. gaillardi* (Ennouchi), *Palaeocryptonyx grivensis* Ennouchi, *Plioperdix grivensis* (Lydekker), *P. depereti* (Ennouchi), *P. joleaudi* (Ennouchi). Of these, all but *Miophasianus altus* are smaller forms than is indicated by the type of *Tantalus milneedwardsii*.

Phasianus altus Milne-Edwards (1869), along with several other forms, was placed in a new genus, *Miophasianus*, by Lambrecht (1933). Later, *M. altus* was designated as the type species of the genus (Brodkorb, 1952). *M. altus* was described from a distal end of a tibiotarsus, a phalanx of the manus, and a proximal end of a tarsometatarsus from the Upper Miocene at Sansan, Département Gers, France. Milne-Edwards (1869) originally characterized it as being a large pheasant about the size of *Crossoptilon auritum*. Depéret (1887) assigned a proximal end of a femur, a proximal end of a tarsometatarsus, three proximal portions of carpometacarpi, and two distal ends of

tibiotarsi from the Grive-Saint-Alban deposits to *M. altus*, stating that the tibiotarsi in no way differed from the holotype tibiotarsus from Sansan. Lydekker (1893) described and figured a proximal end of a tarsometatarsus, a distal end of a humerus, and a complete ulna and carpometacarpus of *M. altus*, also from Grive-Saint-Alban. More recently, Ballman (1969) described the distal end of the femur and other elements from Grive-Saint-Alban, including the distal end of a tibiotarsus which he, too, agreed was identical to the type of *M. altus*. Elsewhere in Europe, a portion of a tibiotarsus from the Upper Miocene of Switzerland (Lydekker, 1891) and wing elements and another distal portion of a tibiotarsus from the Upper Miocene of Germany (Lambrecht, 1921) have been assigned to this species.

The type specimen of *Tantalus milneedwardsii* is, as mentioned, a proximal end of a tibiotarsus. Only the distal end of this element of *Miophasianus altus* has been identified, but as illustrated by Milne-Edwards (1869), it agrees perfectly in size with the type of *Tantalus milneedwardsii*. The measurements of the type of *T. milneedwardsii* are: overall length of fragment 31.6 mm; length of fibular crest 35.3; width of shaft below fibular crest 10.3; depth of shaft below fibular crest 7.9. This suggests a bird larger than *Crosoptilon* but smaller than *Pavo*, i.e. *M. altus*. As no basis exists for assuming that there were two galliform species of this size in the Grive-Saint-Alban deposits, I regard *Tantalus milneedwardsii* Shufeldt 1897 as a synonym of *Phasianus altus* Milne-Edwards 1869.

ACKNOWLEDGMENTS

I would like to thank Pierce Brodkorb for supplying several references, and John Farrand, Jr. for his comments on the manuscript. The photographs are by Victor E. Krantz.

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SYMPOSIUM ON THE BIOLOGICAL RESOURCES OF THE
CHIHUAHUAN DESERT REGION, UNITED STATES AND MEXICO

16-18 October 1974

The Southwest Region of the National Park Service and the Texas Parks and Wildlife Department will co-sponsor and Sul Ross State University, Alpine, Texas, will host this International Symposium. Roland Wauer, National Park Service, and David H. Riskind, Texas Parks and Wildlife Department will act as co-chairmen for the Symposium. Papers to be presented will cover Quaternary environments, botany, mammalogy, ichthyology, herpetology, and ornithology. Invited papers will represent unpublished original research and or unpublished major reviews pertaining to the natural resource data of the Chihuahuan Desert Region. Following the presentation of papers a panel discussion is scheduled in which the necessity for preserving or protecting the biological resources of the Chihuahuan Desert will be emphasized. Conservation measures designed to resolve biological problems and deficiencies in the existing system in both the United States and Mexico will be discussed as well. The panel will be composed of eminent professionals from the United States as well as from Mexico. Dual keynote speakers (representing the U.S. and Mexico) will summarize the earlier comments and present some firm recommendation relevant to resource conservation and management in the Chihuahuan Desert region. The Symposium proceedings will be published in their entirety by the National Park Service. For additional information concerning agenda, registration fees, and accommodations, please address all inquiries to: David H. Riskind, Head, Resource Management Section, Texas Parks and Wildlife Department, John H. Reagan Building, Austin, Texas 78701.

RHEGMINORNIS RESTUDIED: A TINY MIOCENE TURKEY

STORRS L. OLSON AND JOHN FARRAND, JR.

The only fossil form referred to the Jacanidae is the Miocene *Rhegminornis calobates* Wetmore (1943), described from a distal end of a right tarsometatarsus. An interest in that family induced us to restudy this specimen, with the result that it proved to be neither a jacana nor a Charadriiform, but a galliform in the family Meleagrididae. This prompted us to examine other galliform material from the same locality—the Lower Miocene deposits at Thomas Farm, 8 miles north of Bell, Gilchrist County, Florida.

DESCRIPTION AND COMPARISONS

Rhegminornis calobates was assigned to the order Charadriiformes, superfamily Charadriioidea, by Wetmore (op. cit.). It was said to differ from the other groups in that superfamily in the relative positions of the trochleae and in the large scar for the hallux, indicating a much better-developed first toe. Wetmore created the family Rhegminornithidae for the species. He stated (op. cit.:6) that "the fossil shows a stage slightly intermediate between that found in the Scolopacidae and Charadriidae and the Jacanidae. The evident size of the hallux also is reminiscent of the latter family. . . ." This statement led Brodkorb (1967) to consider the species as forming a subfamily (Rhegminornithinae) of the Jacanidae.

The type element of *Rhegminornis* (MCZ 2331) actually shows no resemblance to the specialized tarsometatarsus of the Jacanidae, differing in the greater width of the shaft, in having the inner and outer trochleae much more elevated, the inner trochlea not as enlarged and bulbous, and in lacking the distinct spur on the dorso-lateral corner of the posterior face of the inner trochlea. The scar for the hallux is not as deep: the distal foramen is not located as far distally, is oval rather than circular, and is much smaller, with a much shallower outer extensor groove than in the Jacanidae. The measurements of the type are: width through trochleae 9.5 mm; depth of middle trochlea 4.6; least depth of shaft 2.9; least width of shaft 3.9; overall length of specimen 29.6.

In the relative positions of the trochleae and large scar for the hallux, characters used by Wetmore to establish the family Rhegminornithidae, *Rhegminornis* agrees with typical Galliformes. In the following particulars as well, the type of *Rhegminornis* differs from the shorebirds and agrees with most of the Galliformes.

Inner trochlea.—In posterior view (Fig. 1b), the external side is flat and linear, not rounded nor extending laterally past the line of the internal side of the middle trochlea.

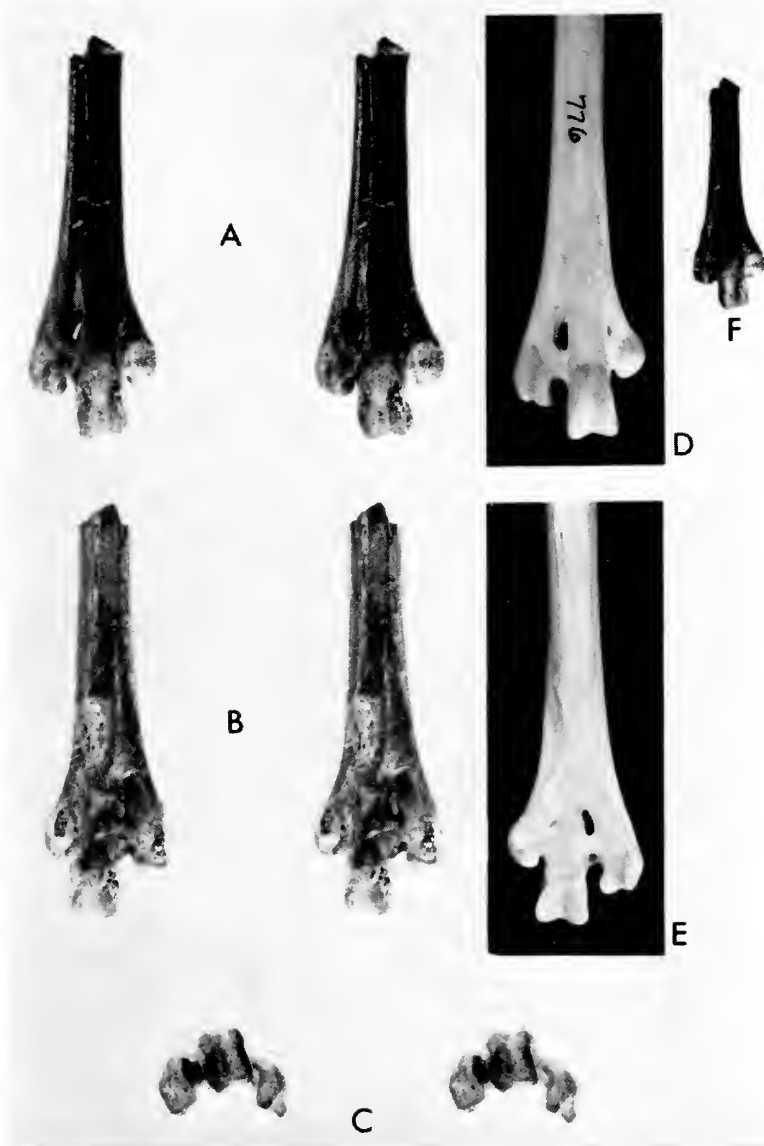


FIG. 1. a, b, c. Stereophotographs of the tarsometatarsus of *Rhegminornis calobates* (holotype, MCZ 2331), about twice natural size (a. anterior view—inner intertrochlear foramen barely visible as a whitish spot; b. posterior view; c. distal view). d, e. Tarsometatarsus of a small female *Melcagris gallopavo*, natural size (d. anterior view; e. posterior view). f. Holotype of *Rhegminornis calobates*, natural size.

In internal view (Fig. 2a), the trochlea forms a distinct bulge distally, with the wing sharply set off from the articulating surface by a distinct pit; the roughened articular surface is much larger and extends farther proximally. In distal view (Fig. 1c), the wing projects more medially rather than directly posteriorly and is more distinctly set off from the rest of the trochlea. As noted by Wetmore, the inner trochlea is not so strongly rotated towards the median axis of the shaft and is thus more nearly in the plane of the other trochleae.

Middle trochlea.—In posterior view (Fig. 1b), the articular surface is more distinctly set off from the shaft of the trochlea, especially on the internal side, and extends farther proximally on the external side. In internal view (Fig. 2a), the internal side is more excavated, with a more distinct rim. In external view (Fig. 3b), the external face bears a squared depression, unlike the deeper more circular pit of the shorebirds.

External trochlea.—In posterior view (Fig. 1b), the shape of the articular surface is quite different from that of the Charadrioidae, with the external side extending much farther proximally. In external view (Fig. 2b), there is a distinct groove on the posterolateral portion of the trochlea to accommodate a ligament attaching the outer toe to the tarsus. This groove is a characteristic feature of the Galliformes but is absent in the Charadrioidae.

These comparisons suffice to remove *Rhegminornis* from the Charadriiformes and place it with the Galliformes. The question of its proper allocation within the latter order may now be explored.

Rhegminornis differs from the Cracidae and Megapodiidae in the following respects: inner trochlea much more elevated, middle trochlea rotated medially, external trochlea more elevated, distal foramen much larger, and the scar for the hallux with a single facet (as opposed to a distinct, polished, circular proximal facet and an elongated, less distinct, distal facet).

From the Tetraonidae it differs in many characters, including the shape and positions of the trochleae, the relatively broader shaft with less expanded distal end, larger distal foramen, and larger scar for the hallux.

Rhegminornis differs from the Phasianidae (sensu stricto) and agrees with the Meleagrididae in the more elevated internal trochlea, larger and more elongate distal foramen, and the presence of a distinct, although small, *inner* intertrochlear foramen. Howard (1927:24) noted that an inner intertrochlear foramen was present in more than half the specimens of *Meleagris* that she examined and that such a foramen, or traces of it, also occurred in *Parapavo* and *Agriocharis* but not in *Pavo*. In *Rhegminornis* the inner foramen is present both anteriorly (barely visible in Fig. 1a) and posteriorly (visible under magnification) in exactly the same position as observed in specimens of *Meleagris* (Fig. 1d and e). We may add here that we did not find an inner intertrochlear foramen in the Charadrioidae. In the tarsometatarsi of *Rhegminornis* and the Meleagrididae, in side view, the middle trochlea curves anteriorly past the line of the shaft whereas in the other Galliformes, including the Phasianidae and the Numididae, the middle trochlea is more nearly in line with the shaft.

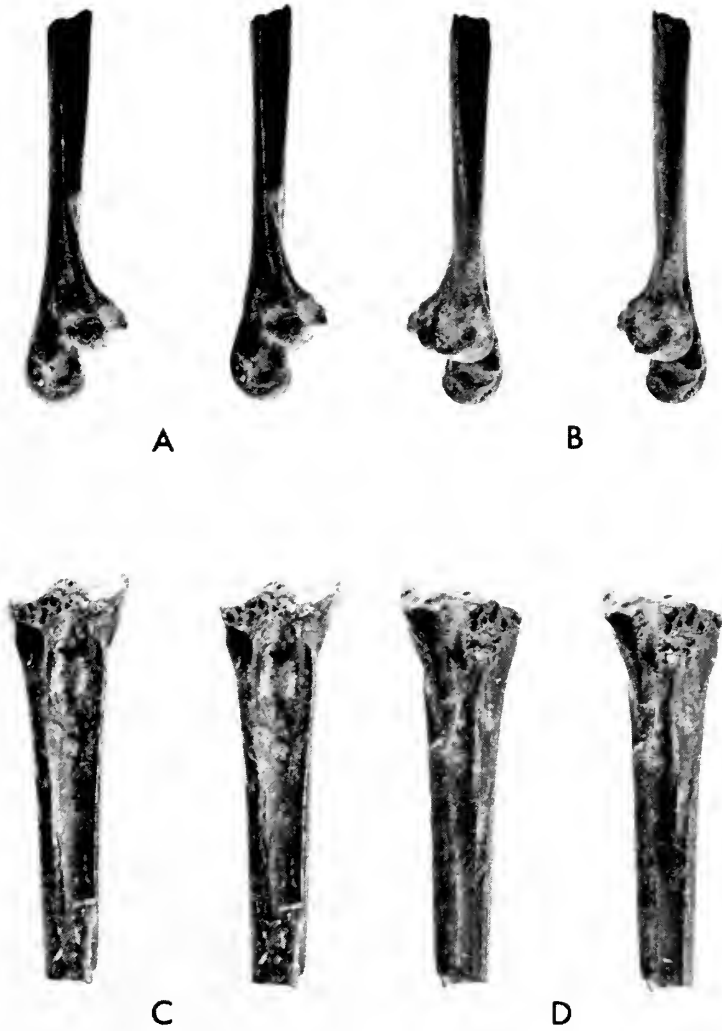


FIG. 2. Stereophotographs of tarsometatarsi of *Rhegminornis calobates*, about twice natural size. a. Holotype (MCZ 2331), internal view. b. Same, external view. c. Referred proximal end (PB 1776), anterior view. d. Same, posterior view.

DISCUSSION

The proper familial allocation of *Rhegminornis* appears to be with the Meleagrididae. It differs from all modern and fossil turkeys in its much smaller size (Fig. 1f) and more elevated external trochlea, but is otherwise

very similar to modern forms. *Rhegminornis* agrees with *Meleagris* and differs from *Agriocharis* (as well as other Galliformes) in the more medially rotated middle trochlea. It more closely resembles *Agriocharis*, however, in having the trochleae less divergent and the distal foramen in posterior view smaller than in *Meleagris* (see Fig. 1).

At least two other bones from the Thomas Farm deposits are referable to *Rhegminornis*. One of these (PB 8447) is another distal end of a right tarsometatarsus, much abraded and lacking the external trochlea; it is virtually identical to the type except that the scar for the hallux is more distinct. The other specimen (PB 8448) is an imperfect proximal end of a right tarsometatarsus (Fig. 2c and d) lacking much of the hypotarsus and part of the external cotyla. This differs from the tarsometatarsus of the Cracidae in the more excavated anterior shaft, the more medial position of the tubercle for tibialis anticus, the much more medially expanded internal cotyla, and particularly in not having the shaft greatly thinned and bladeliike just distal to the internal cotyla as seen in the Cracidae.

In all of these respects the specimen agrees very closely with the Meleagrididae. From *Meleagris* and *Agriocharis* it differs principally in having the shaft somewhat less deeply excavated anteriorly and posteriorly, and in having the tubercle for the tibialis anticus narrower and more clearly defined. The thin, ossified intertendinal septum extending down the shaft from the hypotarsus in modern turkeys and certain other Galliformes is absent in *Rhegminornis*, but this variable feature is probably of little taxonomic significance. Likewise, there is no evidence of a spur in *Rhegminornis*, although this may only mean that the specimens were from females.

From the same deposits at Thomas Farm, a new genus and species of cracid, *Boreortalis laesslei* Brodkorb (1954), was described. The type (PB 743) is a distal end of a right tibiotarsus lacking the internal condyle and the posterior portion of the external condyle. The fragmentary condition of the type and the fact that Brodkorb noted several differences between it and modern cracids suggested the possibility that *Boreortalis* might actually be referable to *Rhegminornis*. This, however, proved not to be the case. In the type of *Boreortalis* the remains of the internal condyle show that it was better developed proximally than in turkeys, with a projection extending over the opening distal to the tendinal bridge—a decidedly cracid feature. Also, the tubercle on the tendinal bridge is more medially located in *Boreortalis* and most cracids than it is in the turkeys.

Furthermore, there is additional unquestionable cracid material in the Thomas Farm deposits. A distal portion of a left tarsometatarsus (UF 2905) shows all the distinctive features of the Cracidae and indicates a species slightly smaller than *Penelope superciliaris*, as does a proximal end of a right

tarsometatarsus (PB 8450). A distal end of a left femur (PB 1776) is from a cracid very slightly smaller than *Ortalis vetula*. The type of *Boreortalis laesslei* was described as being between *Ortalis vetula* and *Penelopina nigra* in size (and is somewhat larger than *Rhegminornis*). It seems possible that more than one species of cracid is represented in the Thomas Farm deposits. In any event, *Boreortalis* is not a turkey and therefore not a synonym of *Rhegminornis*.

Cracraft (1971) has assigned two distal ends of humeri from Thomas Farm to *Boreortalis*. In the better preserved of these specimens (MCZ 7068), the deeper olecranal fossa, the apparently broader and less curved shaft, much less distally projecting entepicondyle, and shallower brachial depression are more similar to *Meleagris* than to the Cracidae. On the other hand, it differs from modern turkeys in having no indentation between the internal condyle and the entepicondyle and in having the brachial depression extending farther distally. These fragments, although slightly larger than might be expected for *Rhegminornis*, are possibly not properly assigned to *Boreortalis*. At any rate, we doubt whether any certain determination can be made of them until better material is available.

Up to now, the oldest known turkey was *Proagriocharis kimballensis* Martin and Tate (1970), from the Upper Pliocene (Kimball formation) of Nebraska. The allocation of *Rhegminornis* to the Meleagrididae extends the fossil record of the family back much farther—into the Lower Miocene. The family otherwise consists of large forms in the genera *Meleagris*, *Agriocharis*, and *Parapavo*, that are represented by several Pleistocene, as well as two modern, species. *Proagriocharis* was smaller than any of the Pleistocene turkeys, and *Rhegminornis* was much smaller yet.

The presence of a small but unmistakable turkey as early as the Lower Miocene suggests that the Meleagrididae have had a long history in North America and may well have undergone considerable radiation during the Tertiary. In view of this, it would perhaps be best to regard warily a number of the fossil taxa described from the North American Tertiary and currently assigned either to the Cracidae or the Tetraonidae. Some of these may well prove to be turkeys.

As determined from study of the various vertebrate fossils from Thomas Farm, the environment in the area at the time *Rhegminornis* bones were deposited there was one of a "river flowing through a dry grass-covered plain" (Brodkorb 1954:182). It is not difficult to envision a flock of diminutive turkeys, clucking and scratching its way along a sparsely wooded Florida riverbank. As the little flock moves on out of sight in the brush at the edge of the plain, a bantam-sized cock occasionally displays in Lilliputian splendor, strutting, gobbling and fanning its tail in the Miocene sunshine.

SUMMARY

The fossil species *Rhegminornis calobates*, based on a fragmentary tarsometatarsus from the Lower Miocene deposits at Thomas Farm in central Florida, has previously been regarded as constituting either a distinct family within the Charadriiformes or a subfamily of the Jacanidae. Re-examination of the type, and two additional specimens of the same element here assigned to the species, shows that *Rhegminornis* is actually a galliform referable to the family Melcagrididae. *Rhegminornis* thus becomes the oldest known turkey and is much smaller than modern members of the family. We suggest that the family Meleagrididae has had a fairly long and diverse history in North America. The allocation to the Cracidae of *Boreortalis laesslei*, another galliform bird from the Thomas Farm deposits, is confirmed. Additional cracid material from the same locality, possibly indicating the presence of more than one species is briefly noted.

ACKNOWLEDGMENTS

We are very much indebted to Raymond A. Paynter, Jr., Museum of Comparative Zoology (MCZ), for allowing us to study the type of *Rhegminornis*, and to Pierce Brodkorb for lending specimens from his own collections (PB) and those of the University of Florida (UF). In this study, as in many others, we have continued to enjoy the counsel and indulgence of our esteemed colleague, Alexander Wetmore. The photographs are by Victor E. Krantz.

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SCALY-LEG (KNEMIDOKOPTIASIS) IN A POPULATION OF EVENING GROSBEAKS

STEVEN W. CAROTHERS, N. JOSEPH SHARBER,

AND

GENE F. FOSTER

Scaly-leg, or knemidokoptic mange, is an avian disease of the feet and beak that has been reported to be a serious problem in poultry and cage birds (Poulsen, 1964). The disease apparently occurs infrequently in wild birds, with isolated incidences having been reported in perhaps a score or fewer species (Louis N. Locke, pers. com.).

At a feeding station in Flagstaff, Coconino County, Arizona, we have observed the disease in three wild species: House Sparrow (*Passer domesticus*), Cassin's Finch (*Carpodacus cassinii*), and Evening Grosbeak (*Hesperiphona vespertina*). In each of the first two species, only one incident of scaly-leg was observed. However, for several years substantial proportions of the local resident Evening Grosbeak population have exhibited the disease.

THE DISEASE AND HOST

The symptoms of scaly-leg include the appearance of small to large, light-colored scabs or encrustations on the beak and/or feet of affected birds (Fig. 1). The development of these scabs is caused by the burrowing of mites (*Knemidokoptes* spp., Sarcoptidae; Fig. 2) into epithelial skin layers, which stimulates the proliferation of excess tissue (Herman et al., 1962). The mites create tunnels that end in pouches, within which both adults and larvae may be found in abundance. The presence of the larvae suggests that the mites complete their life cycle on one host (Yunker and Ishak, 1957) and probably continue to live and reproduce on that host until it is dead.

Since early in 1961, we have been recording the daily occurrence and activities of local birds at the feeding station. During this period, we have recorded a marked change in population size and status of the Evening Grosbeak. Prior to 1963, this species was not observed on a regular basis in the Flagstaff area and was considered by Phillips et al. (1964) to be an erratic and uncommon summer resident in northern Arizona. In February 1964, a flock of about 60 birds took up residence in the pine (*Pinus ponderosa*) forest near the feeding station. Since that time, the Evening Grosbeak has become established in the Flagstaff area as a permanent resident, increasing in total population density at the feeders yearly (see Carothers et al., 1970, 1973). Erratic and irregular invasions occur for many species of birds in response to a variety of natural and/or man-made causes. In this case, the availability of generous and continuous supplies of sunflower seeds, pinyon nuts, millet, and meal worms (Tenebrionidae) at the feeding station were the apparent stimulus for the Evening Grosbeaks to take up residency in the vicinity and to remain throughout the last ten years.

RESULTS AND DISCUSSION

During the spring of 1964, we observed that a very high frequency of scaly-leg occurred among the 60 invading grosbeaks. At this time, it was



FIG. 1. Scaly-leg or knemidokoptic mange in Evening Grosbeaks. A, adult male, heavy infestation, all claws and toes and portions of the lower foot have fallen off; B, adult female, moderate-heavy infestation, note the relatively elongated claws indicating lack of use; C, normal adult female. Photograph by M. Gaede.

estimated that 25 percent of the individuals in the flock had foot abnormalities. The next available detailed records (1967) revealed the disease in 14 percent of the 90 to 95 birds that established residency that year. From 1968 to 1972 no detailed records were kept as to the frequency of the disease, although daily population counts of the Flagstaff flock were continued during the period.

During the early spring of 1973, a concentrated effort was made to band all Evening Grosbeaks that visited the feeding station, using U.S. Fish and Wildlife Service bands. From March through July, 702 adult Evening Grosbeaks were banded and released. An additional 52 individuals (seven percent of the total captured) displayed varying stages of diseased feet and were removed from the population. We estimated that approximately 150 to 200 grosbeaks escaped capture, indicating a probable total spring population of 900 to 950 individuals.

Macro- and microscopic examinations of the diseased birds captured that spring (Fig. 1 and 2) demonstrates conclusively that the disease is caused by the mite, *Knemidokoptes* sp., and not a fungus as previously reported (Carothers et al., 1973).

In the diseased grosbeaks that we have observed, only one case was found in which the beak was affected. This individual was an immature with a quite small (5×5 mm) nodule of the exudate on the upper mandible. In all other cases, the disease was confined to the feet and unfeathered tarsometatarsus. The lesions typically began to form on the proximal end of the tarsometatarsus and extended distally until the entire foot and exposed leg were encrusted with the thick exudate. In many cases, the disease developed to such a degree that portions of the foot were caused to break off and the birds had much difficulty in walking and perching.

Birds with very advanced cases were forced to use the entire ventral

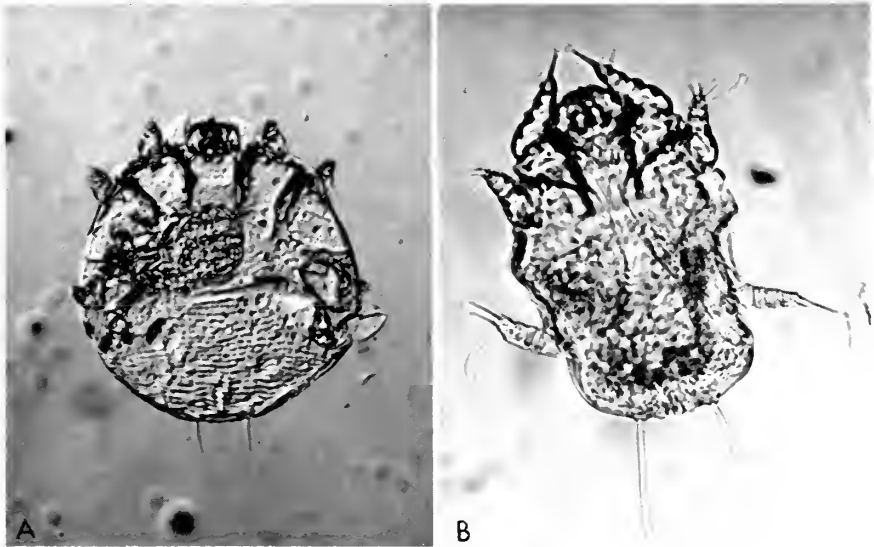


FIG. 2. Photomicrographs of the mite (*Knemidokoptes* sp.) responsible for the disease scaly-leg. A, adult ($\times 250$); B, larval stage ($\times 400$). Photomicrographs by N. J. Sharber.

surface of the tarsometatarsus for supporting their weight, while curling the badly deformed feet up toward the body. In such cases, if the feet were still intact, the claws became greatly elongated from lack of use. The birds characteristically became very subordinate at the feeders: when attacked by other grosbeaks, the former chose to fly short distances, rather than to simply hop away in the manner of non-diseased subordinate birds. Although birds displaying advanced stages of the disease were severely limited in walking and perching ability, none exhibited any serious physiological consequences of having contracted scaly-leg. For example, no significant difference was found between the body weights of healthy and diseased grosbeaks captured during the spring of 1973. Healthy birds had an average body weight of 59.1 ± 0.5 g ($n = 199$) while diseased birds had an average body weight of 58.0 ± 1.3 g ($n = 27$). Also, a comparison of the ratios of gonad weight to body weight among birds captured during the month of May demonstrated no significant difference between the two groups.

The origin of the initial population of grosbeaks that arrived in 1964 is impossible to determine. As noted above, the frequency of scaly-leg in resident populations has slowly declined in nine years, from 25 percent in 1964 to about 7 percent in 1973. The causes of that decline are unknown, but it is likely that a major contributing factor has been our practice of re-

moving diseased birds from the population. To our knowledge, this is the first reported incidence of scaly-leg encountered in near epidemic proportions within a population of wild birds.

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WINTER BIRD DENSITIES ON NORTH AND SOUTH SLOPES

WILLIAM M. SHIELDS AND THOMAS C. GRUBB, JR.

Cantlon (1953), in New Jersey, and Smith (1966), in West Virginia, have shown that, in winter, south slopes are characterized by higher air temperatures and lower wind velocities and relative humidity than contiguous north slopes. Part of this difference stems from greater solar incidence on south slopes. A south slope in North Carolina has been recorded receiving over twice the radiation of a contiguous north slope in winter (Swift and van Bavel, 1961). In New Jersey, these effects produce south slopes that are host to a more xeric forest aspect, with lower values of tree and shrub density and tree basal area (Cantlon, 1953). In view of these differences, we decided to survey the densities of selected resident bird species on a north and south slope in a contiguous forest. As vegetational differences could conceivably affect bird distribution, we surveyed vegetation as well as the avifauna.

METHODS

We worked in the deciduous forest of the Watchung Reservation, Union County, New Jersey. The study area consisted of two ridges, running in an east-west direction, giving the slopes direct northern or southern exposure. We chose six 0.5 mile (0.8 km) transects, 3 each on the north slope (mean height, 165 m; mean slope, 7°) and 3 on the south slope (mean height, 160 m; mean slope, 8°) of parallel ridges. The ridges are at no point separated by less than 0.4 km or more than 1.6 km.

We ran nine bird censuses on each transect, three each in October, November, and December 1972. All censuses were conducted between 07:30 and 10:30, with 20-25 minutes allowed per transect and all transects sampled on each census day. Starting times for each transect were rotated randomly. We counted the six most abundant species, Downy Woodpecker (*Dendrocopos pubescens*), Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee (*Parus atricapillus*), Tufted Titmouse (*Parus bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), and Cardinal (*Cardinalis cardinalis*). All individuals seen or heard within a lateral distance of 412 feet (126 m) were noted. Transect data were transformed into densities using the coefficient of detectability method of Emlen (1971), based on data from both slopes. Probabilities of significance were determined by factorial analysis of variance (Sokal and Rohlf, 1969).

For vegetation analysis, eight 80 m² quadrats were randomly chosen within each bird census plot. Within each quadrat, all trees (D.B.H. > 10cm) were identified and their basal areas calculated. Within each tree quadrat, a 6 m² subquadrat was randomly selected in which all shrubs (D.B.H. > 2.5 cm; height > 30 cm) were identified.

RESULTS

The vegetation sampling showed that the north slope supported 26 species of trees and shrubs, and the south slope 24 (Tables 1 and 2). One species of tree and four of shrubs that occurred on the south slope were absent from

TABLE 1
TREE SPECIES COMPOSITION

| Species | North Slope | | South Slope | |
|--------------------------------|----------------------|-------------------------|-------------|------------|
| | Density ¹ | Importance ² | Density | Importance |
| <i>Quercus rubra</i> | 22 | 78.9 | 19 | 77.4 |
| <i>Liriodendron tulipifera</i> | 16 | 52.1 | 13 | 52.1 |
| <i>Quercus velutina</i> | 3 | 10.6 | 14 | 50.2 |
| <i>Acer rubrum</i> | 4 | 15.1 | 7 | 36.2 |
| <i>Fraxinus americanus</i> | 8 | 20.5 | 6 | 18.7 |
| <i>Betula lenta</i> | 11 | 36.2 | — | — |
| <i>Cornus florida</i> | 1 | 3.0 | 7 | 24.1 |
| <i>Tsuga canadensis</i> | 4 | 11.5 | 3 | 11.3 |
| <i>Quercus alba</i> | 4 | 15.8 | 2 | 8.9 |
| <i>Fagus grandifolia</i> | 8 | 21.1 | — | — |
| <i>Acer saccharum</i> | 4 | 15.7 | 1 | 4.5 |
| <i>Sassafras albidum</i> | — | — | 4 | 11.5 |
| <i>Betula lutea</i> | 2 | 4.2 | 2 | 5.1 |
| <i>Quercus prinus</i> | 2 | 8.0 | — | — |
| <i>Tilia americana</i> | 3 | 7.3 | — | — |
| Total | 92 | | 78 | |

¹ Density is based on the entire 1920 m² area sampled on each slope.

² Importance values are derived by adding the total relative frequency, density and dominance (Curtis and Cottam, 1950).

the north slope; vice versa, the figures were four and three. Two of the north slope dominants, *Betula lenta* and *Fagus*, were absent from the south slope, versus none in the opposite comparison. In addition, the forest of the north slope accounted for slightly more of the total basal area of the two slopes (i.e. 54 percent) and the canopy averaged slightly higher (i.e. 22.5 versus 21.0 m).

All six bird species censused showed significantly higher densities on the south slope ($P < .001$; F-test). The differences in densities between slopes varied between species, with south slope density values ranging from three to more than twenty times north slope values (Table 3).

DISCUSSION

Although similar floristically, the forests on the north and south slope in our study area differ in species composition and in dominants. The south slope is more xeric, having a lesser density of trees and shrubs, lesser tree basal area, and a lower canopy. The differences that we found show the same trend as those found by Cantlon (1953), although his were of a greater magnitude.

The difference in avian densities on the two slopes probably relates to

TABLE 2
SHRUB SPECIES COMPOSITION

| Species | North Slope | | South Slope | |
|------------------------------------|----------------------|-------------------------|-------------|------------|
| | Density ¹ | Importance ² | Density | Importance |
| <i>Viburnum acerifolium</i> | 602 | 108.6 | 168 | 71.6 |
| <i>Cornus florida</i> | 21 | 7.1 | 128 | 64.5 |
| <i>Parthenocissus quinquefolia</i> | 48 | 18.2 | 50 | 27.3 |
| <i>Rhododendron nudiflorum</i> | 70 | 16.1 | — | — |
| <i>Corylus americana</i> | 36 | 16.7 | 2 | 1.9 |
| <i>Gaylussacia baccata</i> | 35 | 7.4 | — | — |
| <i>Hamamelis virginiana</i> | 15 | 9.6 | 10 | 8.4 |
| <i>Rhus radicans</i> | 6 | 5.3 | 8 | 7.9 |
| <i>Vitis aestivalis</i> | 4 | 2.1 | 6 | 4.5 |
| <i>Rubus frondosus</i> | — | — | 8 | 3.4 |
| <i>Cornus alterniflora</i> | 3 | 1.9 | 4 | 2.4 |
| <i>Amelanchier arborea</i> | 6 | 5.3 | — | — |
| <i>Rosa carolina</i> | — | — | 4 | 2.4 |
| <i>Cornus racemosa</i> | — | — | 3 | 2.2 |
| <i>Cornus rugosa</i> | — | — | 2 | 1.9 |
| <i>Vaccinium vacillans</i> | 1 | 1.7 | 1 | 1.6 |
| Total | 847 | | 394 | |

¹Density is based on the entire 144 m² area sampled on each slope.

²Importance values are derived by adding the total relative frequency and density (Curtis and Cottam, 1950).

differences in habitat. What particular aspect(s) of the habitat the birds were reacting to is not so obvious, although one might predict one consideration would be the distribution of plant and/or animal food. The Blue Jay, Tufted Titmouse, and White-breasted Nuthatch all depend on oaks and

TABLE 3
BIRD DENSITIES ON NORTH AND SOUTH SLOPES

| Species | North Slope | | South Slope | | Per-cent ² |
|-------------------------|--------------------------------------|---------------------|------------------|---------------------|-----------------------|
| | Birds Per Mile (1.6 km) ¹ | Birds Per 100 acres | Birds Per Mile | Birds Per 100 acres | |
| Downy Woodpecker | 0.11 ± .10 (6) | 0.6 | 0.82 ± .13 (22) | 4.3 | 79% |
| Blue Jay | 0.93 ± .15 (25) | 3.9 | 4.07 ± .19 (110) | 17.0 | 81% |
| Black-capped Chickadee | 0.93 ± .16 (25) | 4.8 | 4.22 ± .42 (114) | 22.0 | 82% |
| Tufted Titmouse | 0.07 ± .04 (2) | 0.4 | 1.48 ± .19 (40) | 9.0 | 95% |
| White-breasted Nuthatch | 0.41 ± .11 (11) | 2.4 | 1.56 ± .18 (42) | 9.3 | 79% |
| Cardinal | 0.63 ± .16 (17) | 4.7 | 2.22 ± .26 (60) | 16.9 | 78% |
| Total | | 16.8 | | 78.5 | |

¹ ± standard error of the mean (number of birds).

² Percent of total birds counted that were present on the south slope.

beeches for the major portion of the plant content of their diet (Martin et al., 1951). On this basis, the north slope should be more attractive to these species. The plant foods of the Black-capped Chickadee in our study area included eastern hemlock (*Tsuga canadensis*) and poison ivy (*Rhus radicans*) (Martin et al., 1951): as these are about equally abundant on both slopes, any slope preference based on availability of these plants as food seems unlikely. There is some possibility that plant food preference played a role in the higher south slope densities of Downy Woodpecker and Cardinal, as these species depend considerably on dogwoods (*Cornus* spp.), which were more abundant there.

We feel the possibility that the birds were reacting directly to the distribution of prey animals is unlikely. It has been shown that as vegetation becomes more dense, the insect fauna become more abundant (for a review see Lack, 1954). Thus, if insect prey density were the direct determinant of bird density, the north slope, and not the south, should have been preferred.

Although we did not obtain microclimatic data, there is little reason to believe that our study area is substantially different from those studied by Cantlon (1953) and Smith (1966). If this is true, it raises the possibility that during our winter study, the birds were avoiding the greater thermal stress of the north slope and remaining preferentially on the warmer, drier and less windy south slope. In his elaboration on climate-animal interaction, Gates (1969) states that as thermal stress rises, ". . . the homeotherm must adapt primarily by means of physiological adjustment combined with positioning within the habitat." One of the corollaries of Gates' model was the relationship between size of an organism and its susceptibility to thermal stress, i.e. as body size decreases, susceptibility to thermal stress at low temperatures increases. It is therefore reasonable to assume that the small birds we studied conserved energy by tending toward south slopes at low temperatures. Support for this assumption is found on examination of north slope occurrence as a function of mean air temperatures (Fig. 1). For five out of six species, lower air temperatures mean relatively fewer birds found on the north slope. We cannot explain the exception of the White-breasted Nuthatch, although this could be due to sampling error.

In conclusion, we feel that the most obvious factor influencing the avian distributions that we observed was the difference in climate between north and south slopes.

SUMMARY

In the late fall and winter, we conducted a distributional survey of vegetation and of six avian species on north and south facing mountain slopes in New Jersey. Substantial differences in vegetation were found: the north slope supported a denser and more mesic plant community. The birds showed a great preference for the south slope

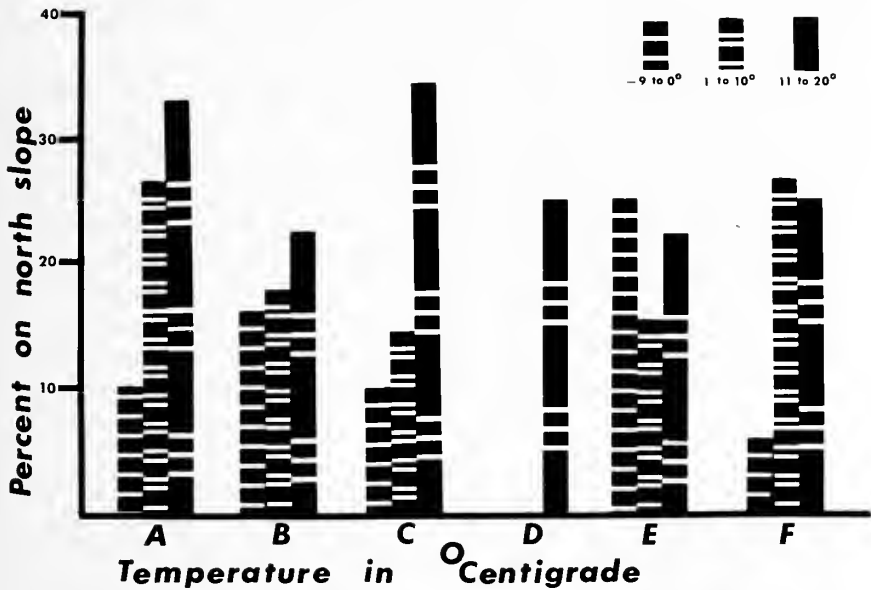


FIG. 1. Percentages on north slope of total individuals of six species counted on both slopes, as a function of temperature. Species A is Downy Woodpecker, B is Blue Jay, C is Black-capped Chickadee, D is Tufted Titmouse, E is White-breasted Nuthatch and F is Cardinal. The -9 to 0° temperature class is based on data from 3 census days, the 1 to 10° class on 4 days, and the 11 to 20° class on 2 days.

(82 percent of sightings for all species combined). We suggest that the birds were attracted to the warmer, drier and less windy conditions on the south slope, with any slope differences in food availability not being a major factor.

ACKNOWLEDGMENTS

We thank J. Burger for help on the figure.

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NEW LIFE MEMBER



Gordon W. Gullion is now a Life Member of the Wilson Ornithological Society. He obtained his B.S. from the University of Oregon and M.A. from the University of California. Presently he is on the staff at the Agricultural Experimental Station at the University of Minnesota. His hobbies include outdoor activities, the most interesting of which is the culture and development of irises! He is a member of several societies, including the A.O.U. and has published about 100 articles—perhaps most notably on gamebirds. Mr. Gullion lives in Cloquet, Minnesota, but grew up in Oregon; he is married and has four daughters and two grandchildren.

RUFFED GROUSE VOCALIZATIONS AT THE DRUMMING LOG

DAVID E. SAMUEL

The male Ruffed Grouse (*Bonasa umbellus*) utilizes an elevated stage, usually a log, to carry out a spectacular performance in which the major sounds are produced by his beating wings. This drumming and other displays have been thoroughly described by Hjorth (1970). The drumming (Fig. 1, Bottom) is of low frequency sounds and is given about every four minutes during its peak, which is 30 minutes before sunrise (Palmer, 1969). Male grouse also utilize vocalizations while on or near the drumming stage. While conducting an analysis of the drums of Ruffed Grouse, I had the opportunity to record these vocalizations, which are presented and analyzed in this paper.

METHODS

These vocalizations were taped while recording 11 grouse in the spring of 1971 and 1972, using the method described by Samuel et al. (in press). The microphone was placed within five feet of the drumming log and operated by a remote off-on switch. Sonagrams were processed through a Kay Electric Company Sona-graph, Model 6061-B, using the wide band pass filter and FL-1 circuit. Irrelevant noise in the recordings was removed from the sonagrams. As direct observations were not made and no experiments were conducted, the functional significance of these calls can only be inferred. One tape was sent to Gordon Gullion, an expert on Ruffed Grouse, for his interpretations which are presented here.

RESULTS AND DISCUSSION

Queet Call.—This call, recorded here as *queet-queet-queet*, was given by seven drumming males (Fig. 1, Top and Middle). In two instances this call immediately preceded drums, three times it preceded flight, and once it was given with an accompanying leaf rustle, indicating movement of the bird near the drumming log. Gullion (pers. comm.) confirmed that the *queet* is “given by a bird that doesn’t quite know what to do,” and “is usually followed by a bird running or flushing.” Aubin (1970) referred to a series of alarm calls (“queet, queet, queet”), immediately preceding flight. Bump *et al.* (1947:97) stated that this same call given just before a bird flushed was an expression of curiosity.

Trills.—On 10 May 1972 a *queet* was preceded and followed by trills (Fig. 2, Bottom). This was the only time a trill was recorded. This bird gave 5 trills, about 50 *queets*, 2 trills, 5 *queets*, and then flushed from the drumming log. The function of the trill is not known to me.

Psst, Hiss, and Whine Calls.—On 5 May 1972 I recorded an encounter between a resident male and a male or female intruder. Various calls were

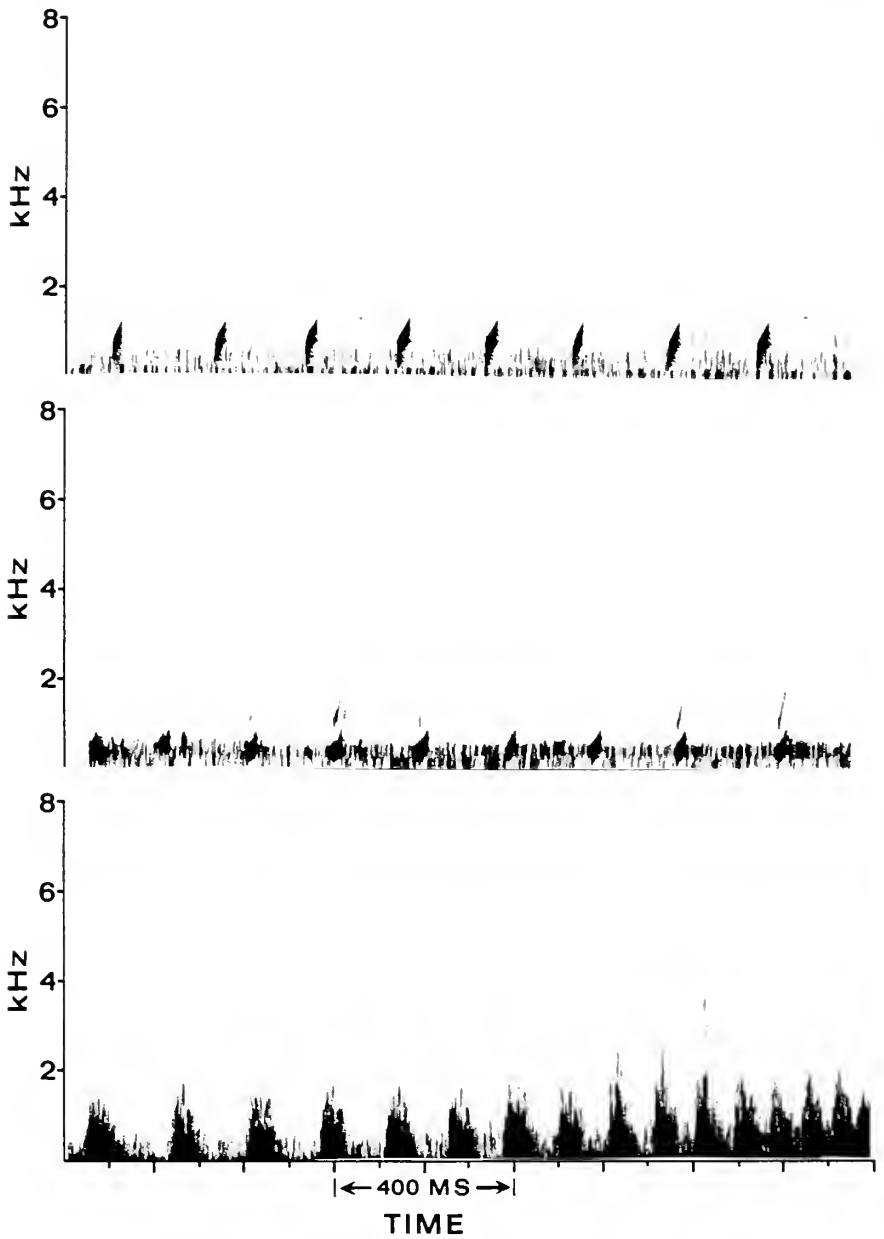


FIG. 1. Top and Middle: The *queet* call given by two different male Ruffed Grouse. Bottom: A small portion of wing beats from a single Ruffed Grouse drumming sequence.

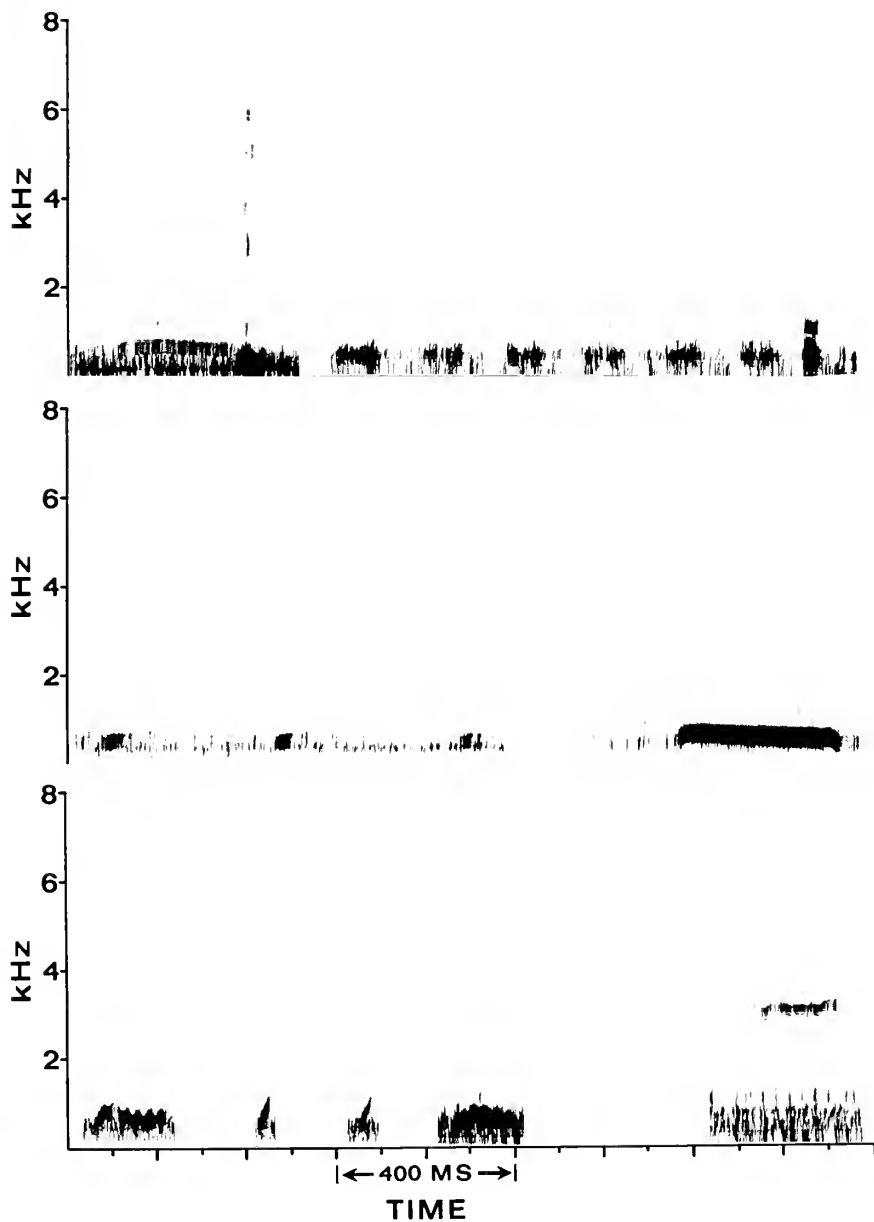


FIG. 2. Top: on left, a "long whine" immediately followed by a single wing beat; on right, a series of hiss calls ending with a pop. Middle: on left, a series of "short whine" calls; on right, a call very similar to the "long whine" call. Bottom: on left, a trill, 2 *queets*, and a trill; on right, a *psst* call.

given and all appeared to come from the resident male. The two minute sequence of events and calls were as follows: first one light *psst* call (Fig. 2, Bottom) was given by the drumming male; the bird then pecked the ground near the microphone for 30 seconds: four seconds of loud leaf rustle was followed by 15 seconds of silence. a drum was followed by a "long whine" (Fig. 2, Top) which was preceded and followed by a single wing beat, a "hiss" (Fig. 2, Top) sounding like a locomotive lasted 5 seconds terminating with a loud pop and an immediate rustle of leaves, a series of "short whines" (Fig. 2, Middle) was given for 20 seconds. This series of vocalizations continued for six minutes and ended with a bird, presumably the resident, continuing his drumming activities. An interpretation of this taped sequence emerges from the review of the literature which follows.

Aubin (1970:31-32) observed eleven grouse interactions, noting "as the resident male approached the intruder, several sharp blows of the bill were directed towards the ground. Following some displacement activity, the resident male usually drums, then rushes at the adversary in intimidation display." Hjorth (1970:235) also discussed behavior associated with an intruder entering a resident territory. He noted the ground pecking and describes the "Bowling cum Head-twisting and Panted Hissing." Rapid head twisting is accompanied by the "hiss" (Fig. 2, Top) which was likened to an accelerating locomotive. Bump *et al.* (1947) stated that this head twisting and "hiss" was followed by a short rush at the female. This could explain the loud leaf rustles heard following each "hiss." No authors refer to the *psst* call, the pop occurring at the end of the "hiss" sequence nor the "short and long whine" calls which were interspersed throughout. During the last minute of this sequence, one bird gave 40-50 *queet* calls, but no sounds of flight were noted.

One other vocalization, similar to the "long whine" (Fig. 2, Top) was recorded at another drumming log on 5 May 1972. This call (Fig. 2, Middle) was much louder than the "long whine." but since it was followed by a single wing beat this difference may have been a reflection of distance from the microphone. After a pause of 30 seconds, he called and gave another wing beat. This continued for three minutes, ending with a drum.

DISCUSSION AND CONCLUSIONS

Hjorth (1970) and Aubin (1970) both present good descriptions of Ruffed Grouse behavior around drumming stages. From my observations, various calls appear to play an integral and as yet not fully determined role in these behavior patterns. Interesting comparisons of these calls can be made with sonagrams from other species given in Hjorth (1970). For example, the "hissing" calls (*op. cit.*:332) of the Black Grouse (*Lyrurus*

tetrix) are very similar in appearance to the Ruffed Grouse "hiss." The Greater Prairie Chicken's (*Tympanuchus cupido*) "whoop" call (op. cit.:381) resembles the "long whine" call, as does the "cackle" (op. cit.:404) given during encounters of male Lesser Prairie Chicken (*T. pallidicinctus*). A complete sonographic analysis of all calls may contribute to our knowledge of phylogenetic relationships within the Tetraonidae.

ACKNOWLEDGMENTS

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FRANK M. CHAPMAN FUND

The Frank M. Chapman Memorial Fund gives grants in aid for ornithological research and also post-doctoral fellowships. Applications are due on 15 September and 15 February. Information on form and content of applications may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

EGGSHELL REMOVAL AND NEST SANITATION IN RING DOVES

WILLIAM A. MONTEVECCHI

Avian nest sanitation includes eggshell disposal, inhibition of defecation on the nest, and the ingestion or removal of nestling fecal matter. Such behavior is widespread among birds, although many different adaptations have evolved in the rearing of offspring (e.g. Blair and Tucker, 1941; Nethersole-Thompson and Nethersole-Thompson, 1942; Pettingill, 1970; Yapp, 1970).

A surprising lack of information exists concerning the defecation patterns of birds (Hailman, 1965; Brackbill, 1972), and only a few systematic studies of eggshell removal have been carried out (Beer, 1960; Hailman, 1966; Thompson, 1970; Tinbergen, 1963). Captive Ring Doves (*Streptopelia risoria*) have been reported to defecate away from their nests during incubation and to remove eggshells from their nests (Miller and Miller, 1958). The present investigation was designed to explore systematically the tendencies of captive Ring Doves to remove eggshells from their nests and to keep their nests free of fecal matter throughout the course of a reproductive cycle. An excellent account of the breeding activities of Ring Doves can be found in Lehrman (1964).

METHODS

Thirty-five pairs of Ring Doves from a laboratory colony were used in this study. All doves were reproductively inexperienced when paired in breeding cages (81 × 46 × 36 cm), which were equipped with a food container, grit container, water dispenser, glass nest bowl (10.8 cm diam., 3.8 cm depth), and straw. Birds were sexed by laparotomy. The pairs were visually but not auditorily isolated from each other, and a photoperiod of 14 hours (06:00-20:00 EST) of artificial light was maintained. Eggshell tests consisted of placing a Ring Dove eggshell in the nest bowl or nest. The eggshells were cracked around the blunter pole to resemble one which remains following the hatching of a squab. The reactions of the doves to the shells were either observed directly through one-way observation windows, or the location of the shell in the breeding cage was checked at 15 minute intervals for a period of one hour. The outcomes of the tests were scored according to the following scale: 1—shell removed within 15 minutes; 2—removal between 15 and 30 minutes; 3—removal between 30 and 45 minutes; 4—removal between 45 and 60 minutes; 5—no removal at the end of the hour test period.

Daily checks were made on the breeding activities of the birds. The tests were administered during the following seven phases of the reproductive cycle: a. prenest test (P)—within approximately 5 days after pairing in the breeding cage (always fewer than 10 straws in the nest bowl); b. nest test (N)—within the period when the depth of straw in the nest bowl was at least 1.25 cm until the first egg was laid (the modal amount of nest material in the nest bowl at test was approximately 2.00 cm); c. early incubation test (E)—counting the day on which the first egg was laid as day 1 of incubation, from day 1 through and including day 5 of incubation; d. mid-incubation

TABLE I
EGGSHELL REMOVALS AND REMOVAL SCORES OVER THE BREEDING CYCLE¹

| | Prelaying | | Incubation | | | Posthatch | |
|------------------------|-----------|-----|------------|-----|-----|-----------|-----|
| | P | N | E | M | L | B | O |
| Number of pairs tested | 26 | 24 | 23 | 16 | 14 | 20 | 26 |
| Number of removals | 8 | 9 | 12 | 9 | 8 | 14 | 17 |
| Percentage of removals | 31 | 38 | 52 | 56 | 57 | 70 | 73 |
| Median removal score | 5.0 | 5.0 | 3.0 | 2.5 | 2.5 | 2.0 | 1.0 |

¹ See methods for explanation of breeding cycle components.

test (M)—from day 6 through and including day 10 of incubation; e. late incubation test (L)—from day 11 through and including day 14 (or the day prior to the hatching of the first egg); f. posthatch brooding test (B)—anytime from the hatching of the first egg (posthatch day 1) until the parents were first observed not brooding the squabs on the nest (approximately day 7 posthatch); g. posthatch nonbrooding test (O)—from the day on which the squabs were first seen unattended on the nest until approximately day 15 posthatch. Most pairs were tested in approximately five of the reproductive phases; successive tests were administered with an interval of at least three days between them. Records of the fecal droppings on the tops of each of the nests were collected during each of these seven reproductive phases.

RESULTS

The percentages of tests during which Ring Doves removed eggshells from their nests increased through successive phases of the breeding cycle (Table 1). Thus, a smaller percentage of the pairs tested in the prelaying periods removed eggshells from their nests than did those tested during the incubation periods, while a greater percentage of the pairs tested during the posthatch periods removed eggshells than did those tested during the incubation periods. The percentage of pairs removing shells during the early, mid, and late parts of the incubation period were very similar. The median removal scores also decreased over the seven successive phase of the reproductive cycle (Table 1).

If an eggshell was removed, removal most often occurred during the first 15 minutes interval (Fig. 1). Observations indicated that most such removals occurred within the first 5 minutes of the test. Sixty-five, sixteen, thirteen and six percent of the removals occurred during the first, second, third and fourth 15 minute interval of the test, respectively. This frequency distribution is significantly different from a random distribution ($P < .01$, Kolmogorov-Smirnov one sample test, Siegel, 1956). The distances to which the shells were removed were found to be least during the prenest period and greatest during the posthatch brooding phase. The severe spatial constraints

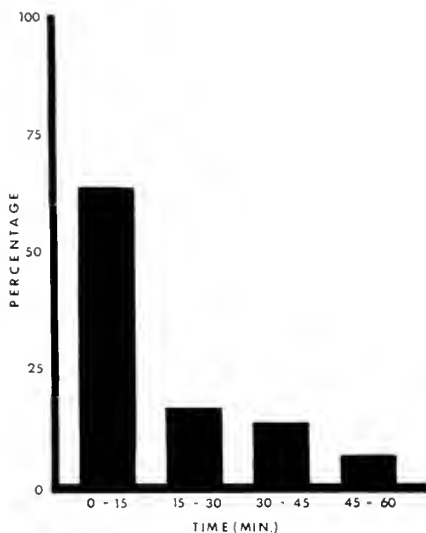


FIG. 1. Percentages of eggshell removals occurring during the different 15 minute intervals of the test.

of the breeding cages precluded any meaningful interpretations from being drawn. Eggshells were flown, walked, and dropped from the nest.

The mean number of fecal droppings in the nest bowl and on the nest varies over the breeding cycle in a manner which may be described as a U shaped function (Fig. 2). A one way nonparametric analysis of variance revealed a significant difference among these seven groups ($F = 7.498$, $df = 6$, $P < .01$). Subsequent Duncan's multiple range tests indicated that the defecation count posthatch phase was significantly greater than those of each of the other six reproductive stages and that the defecation count of the post-hatch brooding phase was significantly greater than those of the mid and late incubation phases; all other paired comparisons were nonsignificant.

DISCUSSION

Ring Doves exhibited an increasing tendency to remove eggshells from their nests over the course of the reproductive cycle. The removal of eggshells increased most markedly around the time of egg-laying, and some evidence exists suggesting a further change in responsiveness toward removal at hatching. The tendency remained remarkably stable throughout the incubation period.

In the prenest tests most doves paid least attention to the nest bowls or to the shell within them, while during the nest tests the doves often incubated

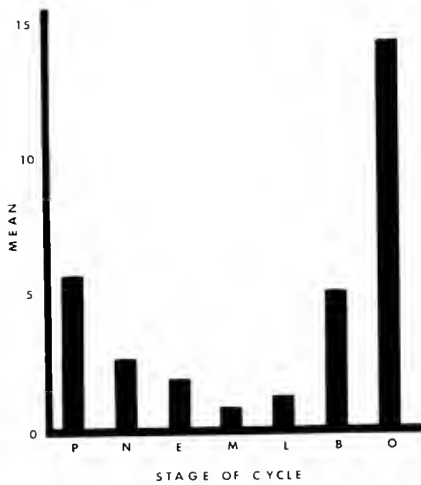


FIG. 2. Mean number of fecal droppings in Ring Dove nests at different stages of the reproductive cycle. Abbreviations explained in text.

the eggshell (seemingly indicative of an increasing tendency to incubate as laying approached). Once a dove laid an egg(s) in the nest, the shell was more apt to be removed. The eggshells were apparently better “differentiated” from eggs, when eggs were present in the nest. The responsiveness of Ring Doves to other sources of external stimulation (eggs, newly hatched squabs) also changes markedly around egg-laying (Hansen, 1966; Moore, 1970). The “tight” sitting behavior of incubation gradually gives way to “looser” sitting patterns of brooding around hatching, and these behavioral changes may be responsible for changes in responsiveness to eggshells in the nest around this time. Doves brooding newly hatched squabs are more likely to arise, look down, and resettle than incubating doves, behavior that may increase the probability of detection and removal of an eggshell. It is well documented that the presence or absence of eggs and/or young in the nest has profound influences upon the responsiveness of birds to many sources of external stimulation (e.g. Lehrman, 1961; Emlen and Miller, 1969; Impkoven, 1973; Cheng, 1973).

The eggshell removal tendency of Black-headed Gulls (*Larus ridibundus*) has been found to increase at laying and to remain high and constant throughout the laying and incubation periods (Beer, 1960:395–408). Beer has also reported that this tendency begins to decline early in the posthatch period of the gulls. Part of the difference between the eggshell removal tendencies of the doves and the gulls in the posthatch period can be attributed to the different patterns of nest attentiveness which species producing altricial and

semi-precocial young exhibit during this phase of the reproductive cycle. Within a few days after hatching Black-headed Gull chicks begin making excursions from the nest: the parents, while still strongly attached to the chicks, become less and less attached to the nest site (Beer, 1966). The doves by comparison remain strongly attached to the nest, until the squabs have fledged. Therefore, differences in the nest proximity maintained by Ring Doves and Black-headed Gull families in the posthatch period may account for the differential eggshell removal tendencies seen between these species during this phase. It should also be noted that the laboratory breeding cages confined *both* Ring Dove parents to the immediate vicinity of the nest, and therefore may have contributed to the species difference reported.

If the doves removed an eggshell during a test, they tended to do so relatively rapidly following the introduction of the shell into the nest. This phenomenon may be widespread among birds: a similar effect has been obtained in eggshell removal experiments conducted with Laughing Gulls (*Larus atricilla*) and Oystercatchers (*Haematopus palliatus*) (Montevecchi, in prep.). This effect is probably due in part to short term habituation process of the birds to a novel stimulus object in the nest.

The adaptive significance of removing eggshells (and other foreign objects) from the nest throughout the reproductive cycle, and particularly at the time of hatching, may differ from species to species. Numerous selective advantages have been postulated to account for the evolution of this behavior, e.g. maintenance of nest camouflage among birds which produce cryptic eggs and young: prevention of interference with effective incubation and brood care: elimination of possible bacteria growth, injury to nestlings, and interference with the hatching success of subsequent other eggs. Ring Dove eggs are white and are continuously incubated (covered) by one parent or the other, which sits tight rather than flees at the approach of an alarming stimulus. Nest camouflage does not seem to have played a significant role in the evolution of the eggshell disposal patterns of Ring Doves.

On the other hand, an unremoved eggshell probably reduces the hatching success of an unhatched egg in the nest. In five of the 24 instances during which eggshells were not removed during incubation period tests, these were found to have fitted over an unhatched egg in the nest by the end of the hour test period. Unremoved eggshells have also been found to entrap unhatched eggs of Tree Swallows (*Iridoprocne bicolor*) (E. H. Burtt, Jr., pers. comm.) and Laughing Gulls (Montevecchi, in prep.).

Once their nests take shape, adult Ring Doves show an inhibition of defecation at the nest which is generally maintained until the squabs vacate the nest. Numerous other species also refrain from defecating at their nests during the incubation period, but Mourning Doves (*Zenaida macroura*)

(Snyder, 1923) and Inca Doves (*Scardafella inca*) (Johnston, 1960) are exceptions. The defecation by those doves on their nests may have adaptive significance, in that the excrement may strengthen their flimsy nests (Skutch, 1964). Fecal droppings occurring on the nest of Ring Doves in this study were due primarily to the excretory activities of the squabs, although adult doves also began to defecate at the nest after the eggs hatched. Adult Ring Doves have been observed eating the feces of nestling squabs, and excrement has been removed from the crops of parental doves (J. Buntin, pers. comm.). Many species of dove are known to eat the fecal matter of their young, and this substance may in turn be fed back to the squabs (Skutch, 1964). As the squabs develop, the amount of feces they excrete increases considerably, and the parent doves make no attempt to deal with this nest fouling.

Like numerous passerines (Yapp, 1970) and other nonpasserines (Nice, 1962), Ring Dove and Rock Dove (*Columba livia*) squabs have been observed to erect their hind ends and defecate over the nest rim (C. Barbieri, pers. comm.). The glass bowls in which the Ring Doves built their nests may have interfered with such behavior in this study. Early in incubation the straw nests often overflowed the bowls, yet by hatching this was matted down and usually contained within the bowl—leaving a glass lip about the nest perimeter. Squab droppings were always found forming a tight circle around the nest edge and on the outer surface of the nest bowl, but never in the center of the nest cup. In a more naturally situated nest, "over the edge" defecation by squabs may have been enhanced.

The study of nest sanitation adaptations in other avian species that remove eggshells from their nests might reveal the generality of the findings that the eggshell removal tendency increases at laying and remains constant throughout the incubation period. Such investigations might also focus upon species whose young show differing degrees of precocity at hatching (thus remaining in close proximity to the nest for different periods after hatching), and on how these adaptations influence eggshell removal and defecation behavior.

SUMMARY

The tendency of Ring Doves to remove introduced eggshells from their nests was investigated over the course of the reproductive cycle. This tendency increased markedly around egg laying, remained constant through the incubation period and showed evidence of a further increase just after hatching. If an eggshell was removed from the nest, it was most likely to have been removed within 15 minutes of its introduction. Comparisons with the eggshell removal tendencies of Black-headed Gulls are made, and the possible adaptive significance of eggshell removal behavior is discussed.

The incidence of defecation at the nest was studied throughout the reproductive cycle. Adult doves refrained from defecating at the nest during the incubation period, although they exhibited a slight tendency to do so during other reproductive phases. Adults

did little to keep their nests clean of the excrement of their young. The squabs showed some evidence of nest sanitation behavior, defecating over the nest rim.

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NEW LIFE MEMBER



David O. Hill is now a Life Member of the Wilson Ornithological Society. He studied biology at the University of Vermont and Harvard, and he is now First Officer on DC-8 jet aircraft. He is an involved member of many wildlife and conservation organizations, with special interests in protection and preservation of marine mammals and of endangered species and habitats in Latin America. His hobbies vary from birdwatching to listening to chamber music. He has had published several articles and photographs, and his travels for birding and photography have taken him from the Arctic to Africa. Mr. Hill is married and lives in Parsippany, New Jersey.

NOTES ON PARENTAL BEHAVIOR AND DEVELOPMENT OF THE YOUNG IN THE WOOD THRUSH

VAL NOLAN, JR.

This paper is based on observations of a pair of Wood Thrushes (*Hylocichla mustelina*) during a single season. It details parental behavior and nestling development and compares this information with previously published data on Wood Thrushes, in particular that of Brackbill (1943, 1958), Kendeigh (1952), and Weaver (1939; in Bent, 1949). In general, the literature is cited without comment where information is consistent with my findings, with discussion reserved for inconsistencies or points of special interest. This is contribution No. 946 from the Department of Zoology, Indiana University.

The pair observed by me built two nests in dry upland woods near Bloomington, Indiana, in 1964. The first of these, which I refer to as the principal nest, produced fledgling young. It was built on a horizontal branch of a large spruce (*Picea abies*), about one m from the trunk and two m above the ground. This nest was two m from a window in my house, and from there my family and I made frequent observations of it. The second nest was located 92 m from the principal nest, and an effort to raise a second brood in it failed. During our observations the weather was mild with little rain; times given are all Eastern Standard.

I netted and color-banded the adults on the day after the nestlings hatched in the principal nest. Only one of the pair had an incubation patch, as reported by Weaver (in Bent, 1949:108) and Brackbill (1958:79) in color-banded birds. This indicates that only the female incubates in this species, contrary to Roberts (1936:121-122) and Todd (1940:442), whose evidence of males' incubating is unsupported and unconvincing. In addition, in my study when the bird that incubated left the nest the other frequently came to the rim and sang but never incubated. I consider the singer to have been the male; hence some observations are ascribed either to the male or the female even before I color-banded the pair.

ARRIVAL TO ONSET OF INCUBATION

The first Wood Thrush was heard in my yard on 18 April 1964, and the principal nest was found on 29 April. Although the nest seemed complete when discovered, a thrush brought material to it several times between 07:30 and 08:00 on 30 April. No further activity was seen until 3 May, when a Brown-headed Cowbird (*Molothrus ater*) laid in the nest before 07:30 and the thrush laid its first egg between 12:30 and 16:30. A thrush, presumably the female, spent the night of 3 May on the nest (see Brackbill, 1958:80), leaving it sometime before 05:30 on 4 May but returning at 06:15, 06:45, and 10:20 and sitting for about five minutes each time. The second thrush egg was laid between 10:25 and 13:50. The assumed female was on the nest continuously from 11:30 until 13:50, and again for a few minutes at 13:55

and 14:45; during 15 other observations prior to 19:53 the nest was unoccupied. A bird was present at 19:53 and on into the night (evening civil twilight was at about 20:11).

On 5 May at 05:25 the nest was unoccupied. I made 15 approximately evenly distributed observations between 05:35 and 10:30, and a bird was present on six. Egg 3 was laid between 10:30 and 13:50, when I observed almost continuously and never saw the nest unoccupied. The female was on the nest on four of my 12 observations between 15:10 and 19:42, all four times after 17:00. At 19:48 she went to the nest and was present into the night. Egg 4 was laid between 11:45 and 16:50 on 6 May. Full-scale incubation attentiveness appeared to begin on that day, as described below.

I obtained additional information about the length of the interval between building and laying and about the hour of laying in 1966, when a nest was apparently completed on 14 May and received its first egg on 18 May. Four eggs were laid, on consecutive days at the following times: egg 1 between 07:30 and 12:00, egg 2 between 11:05 and 12:30, egg 3 between 08:00 and 14:15, and egg 4 between 09:30 and 16:30. Beginning no later than the day egg 2 was laid the nest was occupied by a thrush during the night.

Brackbill (1958:78-79) observed that eggs of this species usually are laid between 09:00 and 12:00 but at times in the early afternoon. He found laying to be earlier on cool days.

FEMALE BEHAVIOR AT THE NEST DURING THE INCUBATION PERIOD

Attentiveness.—On 6 May, the day on which the last egg was laid, the female was on the principal nest on 16 of 26 observations (61.5 percent) prior to 12:00 and on 14 of 19 observations (73.7 percent) between 12:00 and darkness.

From 7 May through 18 May, the day before hatching began, but exclusive of 15 May when the nest was watched all day, I made 284 nest inspections, rather evenly distributed between about 05:30 and nightfall. The female was incubating on 182 of these, or 64.1 percent (see Davis, 1954). This percentage is lower than any of those obtained by Brackbill (1958:81) by pooling periods of continuous observation at each of seven nests; but Kendeigh (1952:135) recorded on a potentiometer that a female Wood Thrush spent only 66.1 percent of three full days (i.e., during daylight) on her nest. The female of the principal nest was present on about 69 percent of 133 inspections made before 12:00 and only 60 percent of 151 inspections made after 12:00, but the difference, tested by chi square, is not significant. There is no significant difference in attentiveness when the data from the first half of the incubation period are compared with those from the second half.

TABLE 1
LENGTHS¹ OF ATTENTIVE AND INATTENTIVE PERIODS² OF FEMALE WOOD THRUSH,
ACCORDING TO TIME OF DAY

| Time of day | Attentive periods | | | Inattentive periods | | |
|-------------|-------------------|-----------|-----------|---------------------|-----------|----------|
| | n | \bar{x} | extremes | n | \bar{x} | extremes |
| 05:17-07:59 | 7 | 18.2 | 27.5-11.5 | 8 | 4.4 | 8.0-1.5 |
| 07:59-11:02 | 7 | 19.1 | 26.0-14.5 | 7 | 7.0 | 10.0-5.0 |
| 11:02-14:08 | 4 | 36.3 | 115.5-6.0 | 4 | 7.5 | 9.5-5.0 |
| 14:08-16:59 | 6 | 19.0 | 35.0-4.0 | 6 | 11.3 | 17.0-6.0 |
| 16:59-19:45 | 6 | 17.7 | 25.5-12.0 | 6 | 10.0 | 13.0-4.0 |

¹ Lengths are in minutes, rounded to the half-minute.

² Data were obtained by a continuous observation from the beginning of the first attentive period to the end of the last inattentive period on 15 May, the tenth day of the incubation period.

A continuous watch was carried out on 15 May, which was fair with extreme temperatures of 79° and 45° F. On the preceding evening, the female had retired to the nest at 19:25, about 55 minutes before civil twilight (compare Kendeigh, 1952:Table 32). She left it for the first time on 15 May at 05:17, about 14 minutes after civil twilight (compare Kendeigh, loc. cit.). Her attentive period during the night had lasted 9 hours and 52 minutes (see Brackbill, 1943:75). She returned to the nest for the night at 19:45 on 15 May; the interval between the beginning of her first attentive period and the end of her last inattentive period was 14 hours and 47 minutes long.

The number of attentive periods on 15 May was 30 and of inattentive periods 31, which represents a more frequent alternation of attentiveness and inattentiveness than those of two females monitored by Kendeigh (1952:loc. cit.) with a potentiometer. Some of Brackbill's (1953:81) data are more consistent with mine but were not obtained by day-long observation. The mean length of the 30 attentive periods was 20.9 minutes, with a standard deviation of 19.2 minutes. (Lengths of attentive periods were not normally distributed; the median length was 17 minutes.) The mean length of the inattentive periods was 7.8 minutes, with a standard deviation of 2.4 minutes. The female was sitting on or standing over the nest during 626.5 minutes of the 868 minutes between 05:17 and 19:45, or 72.2 percent of the time (see Kendeigh, 1952:134-137). Assuming that she was continuously attentive at night, she was on the nest 1198.5 minutes of the 1440 minutes making up the calendar day of 15 May, or 83.2 percent of the 24 hours. However, on 115 occasions while I watched her, she rose to turn eggs, to shift position, to preen, to pick at the nest, or to stand over the eggs (Brackbill, 1953:82). These movements, during which no heat was applied to the eggs, consumed about 90 minutes.

Attentiveness on 15 May varied according to the time of day. To show this, I have divided the daylight period into five intervals, each approximately three hours long. The intervals begin and end a few minutes before or after, rather than exactly on, the hour because this permits me to start and end intervals with the onset of an attentive or an inattentive period. Table 1 shows for each interval the number, mean duration in minutes, and extreme lengths of attentive and inattentive periods, rounded to the half-minute.

The long attentive period and the high percentage (83 percent) of attentive

time in interval 3 was doubtless associated with the fact that the sun shone directly on the nest from 11:00 to 13:30. During the other intervals the attentive periods were much shorter and showed considerable similarity. Inattentiveness was greatest during the afternoon and evening (37.4 percent in interval 4, 35.9 percent in interval 5); this decline in attentiveness was produced by increasing the length of the inattentive periods while holding the length of the attentive periods roughly constant. These results differ from those of Kendeigh (1952:136-137), who found that two females incubated least between 08:00 and 16:00.

Behavior other than incubation.—Other behavior of the female at the nest on 15 May consisted of dozing, preening, egg turning, examining and picking at objects (perhaps parasites), tugging vigorously and persistently at something in the cavity, and changing the direction in which she faced. Dozing, which usually began shortly after inattentive periods ended, was not noted after 09:20. It ordinarily lasted about 30 seconds, but at 08:00 the female appeared to doze for about seven minutes. Preening was recorded 18 times between 07:51 and 20:00, most frequently during the long mid-day attentive period. The mean duration of bouts of preening was about one minute, the longest about four minutes. Egg turning behavior consisted of thrusting the head and bill beyond the eggs and then drawing the bill backward in a raking motion (see Weaver, in Bent, 1949:103); doubtless there was also some moving of the eggs whenever the female changed positions. I counted about 115 movements that probably caused some shifting of the eggs.

During the long period on the nest in the middle of the day the female appeared to be in considerable discomfort. Much of the time her bill was open about ten mm at the tip, and she seemed to pant (see Weaver, in Bent, 1949:114). She frequently raised the feathers of the crown, which occasionally remained erect for several seconds but at other times rose and fell in a slow rhythm.

The direction in which the female faced while sitting on the nest was recorded after each return to it as well as after nearly all occasions on which she rose to turn or inspect the eggs, pick at the nest, etc. There was a significant ($P = <0.01$) preference for facing away from the house, two walls of which joined to form a right-angled sheltered space in which the nest tree stood. Routes in leaving the nest and returning to it varied little and probably were dictated by the position of the house.

On 15 May the female arrived with a caterpillar at 10:35, looked into the nest, ate the caterpillar, and settled on the eggs.

In addition to the observation that her last inattentive period ended at 19:25 on 14 May and 19:45 on 15 May, I recorded four other times of re-

tirement during incubation, viz., 19:44, 19:39, 19:36, and 19:35. On another evening the female was on the nest when I looked at 19:15 and was still present when I quit watching after dark.

MALE BEHAVIOR AT THE NEST DURING INCUBATION

Increasingly as the incubation period advanced, the male perched on or near the nest when the female was absent. During the first two days of the period I did not see this behavior on 21 inspections made when the female was absent: the next two days the male was at the nest in three of the 18 inattentive periods of the female that I observed; in the last half of the incubation period he guarded the nest during about 60 percent of the observed inattentive periods. Brackbill (1943:75-76; 1953:83) witnessed males guarding nests with considerably greater regularity than this, but Weaver (in Bent, 1949:111) found much variation among males.

The day-long watch on 15 May provided details of the male's guarding behavior. He went to the nest during 18 of the 31 inattentive periods (standing on the rim for 123 minutes of the 241.5 total minutes that the female was away), perched within a few meters of it on two others, and foraged on the ground just below it on yet another. His earliest visit began at 07:07, his latest at 19:36; the shortest lasted one minute, the longest 17 minutes. Except twice when the female's departure and male's arrival were simultaneous, he appeared at the nest from 15 seconds to several minutes after his mate had left. He remained until she returned, occasionally leaving a second or two before she alit. Six times he stayed within a meter or so for from 30 seconds to two minutes after the female had resumed incubating, and once he stood on the rim for five seconds after she had entered the nest.

The male sang during all but five of his visits to the nest on 15 May (see Brackbill, 1943:76); four of the silent episodes occurred in the afternoon. The number of songs per visit varied from one to 111, the latter number during a visit lasting slightly over seven minutes. The total number of songs at the nest that day was 352, most sung at normal volume but some quite faintly. Singing invariably stopped when a potential intruder appeared.

Other behavior of the male consisted of occasional picking at objects in the nest and, once, persistent nervous flirting of his wings. On 6 May he brought food and offered it to the female. She rose and perched on the rim: the object seemed to fall into the nest, whereupon the female poked into the cavity and may have eaten it. On 15 May, the male brought food and passed it to the female (see Weaver, in Bent, 1949:108-109). She ate it, and he left immediately. Bent (1949:147) reports that the male Hermit Thrush (*Catharus guttatus*) brings much food to his incubating mate. This feeding of the female may account for Bent's observation (op. cit.:149) that an incubating female Hermit Thrush left the nest at no other times except early morning and just before sunset.

REACTIONS TO OTHER ANIMALS

With rare exceptions the many birds that approached the nest were completely ignored. Most notably, a pair of Robins (*Turdus migratorius*) built a nest five m from the principal nest and at about the same level. Between 1 May, when the Robins' building began, and 17 May, when a predator took their eggs, the two pairs of turdids were often close to each other; but I saw no agonistic behavior or any other interaction. Brackbill (1943:83) found that a pair of Wood Thrushes were tolerant of Robins nesting about 16 m from the nest of the former. These observations contrast with Weaver's (in Bent, 1949:104) report that Wood Thrushes usually fight Robins and actually exclude them from the territory (1939:19). Also ignored were House Wrens (*Troglodytes aedon*), Gray-cheeked Thrushes (*Catharus minimus*), House Sparrows (*Passer domesticus*), Cardinals (*Cardinalis cardinalis*), and White-throated Sparrows (*Zonotrichia albicollis*). House Sparrows, foraging within 0.3 m of the Wood Thrush nest, caused the branch on which it rested to jiggle without eliciting the slightest response. The female's crown feathers rose (see Weaver, in Bent, 1949:114; Dilger, 1956:326-331) and she occasionally looked down alertly when a bird made a sudden noise on the ground beneath her, and once the male appeared to look around cautiously when a Blue Jay (*Cyanocitta cristata*) called several times nearby. A day or two later when a Blue Jay called about 17 m from the nest, a Wood Thrush, probably the male, flew directly at the jay and chased it away.

Cottontails (*Sylvilagus floridanus*) and frequent chipmunks (*Tamias striatus*) passing under the nest were watched alertly, as were chipmunks that climbed into the nest tree. When a house cat (*Felis catus*) walked below her nest, the female rose slightly and sat with neck extended, tail and bill pointed about 45° above the horizontal (see Weaver, in Bent, 1949:105). Similarly, when a fox squirrel (*Sciurus niger*) jumped from the house into the nest tree while the male was on the nest rim, the thrush pointed his bill straight upward and became motionless. He maintained this pose even after the squirrel had moved away and apparently out of his line of vision; his head returned gradually to its usual position a minute or so later. A squirrel jumped into the tree while the female was standing in the nest, and she immediately settled on the eggs. Passing children caused the female to raise her bill to a 45° angle and to erect her crown feathers. My occasional visits to the nest led both birds to attack me, flying close to my head and calling both the familiar *quit* note and a plaintive descending note resembling *whew*. The male and perhaps the female snapped the bill loudly when passing my head (see Weaver, in Bent, 1949:115; Dilger, 1956:326-331).

HATCHING: DURATION OF INCUBATION

Eggs 1 and 2 disappeared during incubation. Egg 1 was on the ground below the nest, broken and dried, when a chipmunk ate it shell and all on 15 May. The cowbird egg never hatched and disappeared on 25 May.

Egg 3 revealed a small projecting bump with a discolored (dried) area around it at 12:48 on 18 May, and pipping of egg 4 began to be evident at about 16:00 the same day. Neither egg had hatched at darkness. I frightened the female off at 05:16 on 19 May and found that egg 3 had hatched. The shell was present, the nestling still in half of it (compare Brackbill, 1958:81); an adult removed one of the halves at 05:20 and the other was carried away one minute later, possibly by the same bird. Brackbill (1948:76; 1958:81) and Weaver (in Bent, 1949:109) noted the carrying away of egg shells: Weaver saw a female eat a shell.

Egg 4 hatched at about 05:35, about 14.5 hours after it pipped. Weaver (1949:109) reports a similar and also a somewhat longer interval. The male, the only adult present when egg 4 hatched, poked at the nest's contents for five minutes, then carried half the shell away. In ten seconds one of the pair landed on the rim and in two minutes flew away with the remainder of the shell.

The incubation period of egg 4 was 304 hours and 18 minutes, i.e., about 12.7 days, plus or minus a maximum error of 2 hours and 32 minutes (half the length of the interval between the two inspections during which egg 4 was laid). Weaver (in Bent, 1949:107-108) states that the incubation period of two nests was 13-14 days long, but details that she presents indicate that the last egg took only about 13 days to hatch. Brackbill (1958:81-82) reports incubation periods almost identical in length to that of the principal nest.

CARE OF THE NESTLINGS

On the day the eggs hatched the female returned to the nest without food at 05:21, left after 12 minutes, returned without food after nine minutes, left after five minutes, and came back six minutes later at 05:53 with a green caterpillar too large for the nestling to eat (see Brackbill, 1958:83). Between 05:21 and 05:53 the male came to the nest three times without food and probed silently into the cavity. At 05:54 he returned with a caterpillar, which the female accepted and ate. The male then removed from the nest the large green caterpillar that his mate had brought earlier, and she took this from him too and ate it. The older nestling ate first at 06:24, over one hour after I discovered it, and again at 06:41. The female brought these items: the male had visited the nest four more times by 06:41 but had brought no additional food.

Between the day when the young hatched and 31 May, when they left the nest, I made approximately 150 observations as I passed the window. On about 145 of these there was an adult present: most of the exceptions were between 19:00 and 20:00. After I had color-banded the pair, I noted the sex

of the bird in attendance; among 82 cases, the female was present 58 times and the male 24 times.

On the fourth day of life of the young, I watched the nest from 07:15 to 11:34. The female was present 75.8 percent of the 264 minutes but spent a considerable part of this time standing, looking at and poking the nestlings, delivering food, eating feces, and preening. Her attentive rhythm was much slower than it had been on the day-long watch during incubation, although the weather was very similar. Her full periods at the nest lasted 30, 50, and 64 minutes; two incompletely observed periods lasted more than 19 and 37 minutes. Inattentive periods during this observation were 6, 13, 21, and 17 minutes long. The male visited the nest ten times and was on the rim for 53.5 minutes of the female's 57 minutes of absence (see Brackbill, 1958:84; Harbaum, 1921). He provided most of the food (see Brackbill, 1943:77), at least eight loads as compared with the female's three, and the amount brought per load appeared to be much larger than the female's. Sometimes the items were single large caterpillars or moths, but on at least three visits he brought three or four items at a time, appearing to regurgitate those carried in the back of his mouth. Regurgitation of food for the nestlings has been attributed to the Hermit Thrush (McClintock, 1910:411) and to Swainson's Thrush (Stanwood, 1913:131). At times the male Wood Thrush passed his food to the female to be delivered; occasionally he divided it with her. Both adults ate occasional surplus items.

All fecal sacs were eaten, at least four by the female and two by the male; evidently Wood Thrushes carry few sacs away, at least until the nestlings are well grown (see Weaver, in Bent, 1949:110-111; Brackbill, 1943:79-80; 1958:83-84). The young did not always defecate immediately after feeding. Once the female ate a sac 12 minutes after the most recent delivery of food.

The female spent every night on the nest while the young were present. Until they were large, I weighed a nestling just before dark each evening. This disturbance precluded obtaining information about the female's normal retirement time, but it probably would have been later than it had been during incubation. One night she fed the young at 20:10; and on the last three days of the nestling interval, when I did not weigh the young, she retired at 19:57, 20:11, and 20:11 (this last was about 25 minutes before civil twilight).

NEST LEAVING: DURATION OF NESTLING INTERVAL

The older nestling left the nest at about 13:15 on 31 May, the younger at 13:35. The latter perched on the nest rim at 13:30 and was fed there at 13:34. One minute later it hopped a few cm out on the nest branch. After a further minute it moved another 15 cm away; its sibling was then two m from the nest. The younger bird weighed 36.0 g at nest leaving, the older only 30.1 g. The two were able to hop along the ground very quickly; occasionally, however, one tottered and fell in its haste. They appeared to be able to fly only about 0.3 m. Brackbill (1943:80) observed flights of about 16 m by young just out of the nest.

TABLE 2
WEIGHTS OF WOOD THRUSH NESTLINGS,¹ ACCORDING TO 24-HOUR INCREMENTS IN AGE²

| Approximate age in hours | Weights per nestling, in grams | | |
|--------------------------------|--------------------------------|-------------------|------|
| | 1 | 2 | 3 |
| 0.5 | 3.8 | — | 4.2 |
| 24 | 5.0 | — | 5.8 |
| 48 | 7.9 | 6.7 | — |
| 72 | 11.3 | — | 14.3 |
| 96 | 15.6 | 14.1 | 17.0 |
| 120 | 20.3 | 17.6 | 21.2 |
| 144 | 24.3 | 21.1 | 24.9 |
| 168 | 25.6 | 25.0 | 28.5 |
| 192 | 29.3 | 26.8 | 31.5 |
| 216 | 31.7 | 29.5 ³ | — |

¹ Bird 1 was the younger nestling from the principal nest, in which there was one other nestling. Birds 2 and 3 were nest mates from a brood of three.

² Weighing stopped when the birds reached the age at which they could no longer be handled without causing premature nest-leaving.

³ The third member of this brood, not otherwise dealt with in this table, weighed 28.6 g at this age.

The older bird spent about 296 hours and 5 minutes, i.e., about 12.3 days, in the nest after hatching, the younger exactly 294 hours and 55 minutes. In 1965, I recorded the approximate length of nest life of one young Wood Thrush from a brood of three. It left the nest 299 hours and 45 minutes, plus or minus about 10 hours, after hatching. These intervals in the nest accord with those reported as typical by Weaver (in Bent, 1949:109). Brackbill states (1943:80) that young fledged prematurely after ten days, but in his later paper (1959:84) he gives 12 to 14 days as the normal age at which he observed nestlings depart.

WEIGHT OF EGGS AND NESTLINGS

The last egg laid in the principal nest weighed 4.8 g no longer than four hours after it was laid. At 07:00 on the day before it hatched, before pipping began, it weighed 4.1 g, having lost 15.5 percent of its original weight. Slightly more than an hour before it hatched, when the cracks in the shell had certainly caused some drying of fluids and consequent weight loss, it weighed 3.9 g.

Table 2 shows the weights of three nestling Wood Thrushes at approximately 24-hour intervals during that part of their nest life in which I could handle them. Bird 1 in the table was the younger nestling in the principal nest. Birds 2 and 3 were two members of the 1965 brood referred to in the

preceding subsection. Weights were taken at about 07:00 and 19:00; they changed very little overnight. Weaver (in Bent, 1949:110) reports that a newly hatched Wood Thrush weighed about 5.1 g, relatively much heavier than the young birds I examined.

DEVELOPMENT OF PLUMAGE

The neossopiles of a nestling from the principal nest were dark gray at hatching; this description is not based on a color chart. I counted six over one eye, seven over the other. The occipital pteryla bore two neossopiles on each side of the head, the spinal pteryla 15, the humeral two on one side and one on the other. This pattern differs greatly from the pterylosis described by Wetherbee (1957:414-416) as the basic pattern for the Turdidae.

At the age of 48 hours the femoral, humeral, spinal (excluding the cervical region), and alar tracts of the nestlings were visible beneath the skin. Twelve hours later the capital tract was becoming visible, and the tips of the primaries projected very slightly. At 72 hours the tracts and regions previously visible had become more conspicuous. The ventral and crural tracts still could not be seen, but 12 hours later both were discernible.

At 96 hours the primary sheaths projected about 2 mm, the secondary sheaths 1 mm, and some secondary coverts were just emerging. The interramal, malar, sternal, axillar, and abdominal regions were becoming visible beneath the skin. Sheaths of tracts that had been visible earlier were now about to emerge from the skin.

At 120 hours the primaries were about 5 mm long, the secondaries slightly shorter; the greater coverts of these two regions and the alula feathers were about 3 mm long. Femoral, humeral, spinal, and some anterior ventral quills projected beyond the surface of the skin. Twelve hours later feathers of the capital and crural tracts and the middle secondary coverts had just begun to project. Some primaries and secondaries were 10 mm long.

At 144 hours feather tips showed beyond the sheaths of the greater and middle secondary coverts. Twelve hours later the tips of feathers showed from all sheaths but those of the capital and crural tracts, the primaries and secondaries, and the interramal and malar regions.

At 168 hours the primaries and secondaries were 17 to 20 mm long, still fully sheathed. Twelve hours later the primary sheaths were about 21 mm long, with feather tips projecting. The spinal feathers were growing, and the dorsal surface of the birds no longer looked bare; the color was fuscous. Colors referred to in this and the next paragraph were obtained by placing the bird next to a color chart (Palmer, 1962:chart following 4) and judging accordingly. The anal circlelet was noticed for the first time; it consisted of well-developed quills.

At 192 hours the dorsal surface of the body and wings was brownish olive, except that the scapulars were sepia. The secondary coverts were brownish olive with tawny tips. The capital feathers, now rapidly emerging, were brownish olive on the frontal and anterior coronal regions, rufous posteriorly. The belly was light cream. The primaries and secondaries were about 25 mm long, about 4 mm of this consisting of feather tips. Twenty-four hours later these alar feathers were about 31 mm long, half sheath and half feather tip. The plumage changed little in appearance thereafter. The gape was

orange on the lower mandible, orange yellow on the upper. The darkening mandibles were largely fuscous, the tip sepia; the rictal flanges were buffy yellow to cream; flesh tones still showed around the nares.

When the young left the nest the primaries were about 45 mm long, and the bent wing, flattened and measured in the usual way, was 67 mm.

DEVELOPMENT OF BEHAVIOR

At age 96 hours the eyes had not yet opened, but at about 108 hours they opened slightly when the young gaped (see Weaver, in Bent, 1949:110).

At 144 hours the young clung to the nest lining when handled. At 168 hours they uttered faint calls during weighing. A few hours later they gave a rapid series of calls whenever handled. At about 200 hours, however, nestlings still showed no fear of me and gaped at my hand when I placed them on a balance.

Not till age 240 hours did the young move about much in the nest (see Weaver, in Bent, 1949:111). They then became exceedingly active, preening, scratching (the foot over the wing), fanning the wings, stretching, and getting to the nest rim for a few seconds. These activities were especially frequent when the sun shone on the nest.

SECOND-BROOD AND REPLACEMENT NESTING

On 16 June the pair from the principal nest apparently were no longer caring for their fledglings, which on that day were about 28 days old (see Brackbill, 1958:85). On 3 July I discovered the female sitting on a new nest, about three m above the ground. When I first examined it closely late on 4 July, the nest held only two cowbird eggs; by 19:00 on 5 July these had hatched. The nest failed on 9 or 10 July and I saw no subsequent evidence of breeding, although I have found Wood Thrushes about six days old and still in the nest at Bloomington as late as 22 August. Production of second broods has been reported for pairs of color-banded Wood Thrushes (Brackbill, 1943:74, 81; 1958:85; Weaver, in Bent, 1949:112).

The incubation of the cowbird eggs that hatched on 5 July probably began on about 24 June. If the female thrush built this nest in three or four days, waited two or three days, and then laid two or three eggs, she must have begun to build the second-brood nest approximately in the period 17-19 June, i.e., some 17 to 19 days after her first brood left the nest. Brackbill (1958:79) observed several cases in which the interval between these events apparently was no longer than four or five days, and Harbaum (1921) saw an unbanded female building within three days of a first brood's nest-leaving (but see Brackbill, 1943:74, and Weaver, 1939:22).

SUMMARY

A Wood Thrush nest appeared to be complete when found, 12 days after the male first sang on the territory. Three days then passed before laying began. Four eggs were laid on consecutive days, probably all of them at about noon. Only the female appeared to incubate; she spent every night on the nest after the first egg was laid. According to one method of sampling, the female spent about 64 percent of the daylight hours on the nest during the incubation period; on a day when the nest was watched continuously she was present 72 percent of the time and left the nest 31 times. The male often perched on or near the nest and sang when the female was absent. Behavior of the pair toward birds and other animals is described. The incubation period was about 12.7 days, and the two young that hatched left the nest when slightly over 12 days old. The weights of the nestlings at various ages are presented, and the development of the plumage and certain nestling behavior are described. The female began a second-brood nest about 17 to 19 days after the nestlings left the first nest, but this effort was unsuccessful.

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AVIAN EGG SHELL THICKNESS: VARIABILITY AND SAMPLING

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Studies comparing recently collected eggs with those in archival collections have shown that shell thickness in certain predatory (including fish-eating) birds has decreased significantly since the introduction and widespread use of persistent chemical insecticides, particularly DDT (Ratcliffe, 1967, 1970; Hickey and Anderson, 1968; Anderson and Hickey, 1970, 1972; Peakall, 1970; Blus, 1970; Blus et al., 1972; Koeman et al., 1972). This decrease in shell thickness is correlated with reproductive failures in some of these species, with populations declining when thinning persists for a period of years. Baseline data on eggshell thickness depend on studies of archival egg collections, which have had few additions since the 1930's—when severe restrictions were placed on egg collecting as a conservation measure. For more recent data, interested researchers must often collect eggs themselves, and they are faced with many problems. These include optimal allocation of time and resources to obtain adequate samples, while minimizing the impact of egg collecting on the reproduction of a species.

We feel that a knowledge of the variability of shell thickness in species is essential to determination of the proper size and composition of samples. To illustrate this, we have measured and analyzed eggs in museum collections of the following: Black-crowned Night Heron (*Nycticorax nycticorax*), White Ibis (*Eudocimus albus*), Clapper Rail (*Rallus longirostris*), Mockingbird (*Mimus polyglottus*), and Loggerhead Shrike (*Lanius ludovicianus*). Our analyses of these data are intended (1) to probe the variability in eggshell thickness and to discuss some of the factors which contribute to this variability; (2) to show how a knowledge of variation can enable one to estimate sample sizes needed for detecting specified differences in shell thickness; and (3) to discuss the advantages and disadvantages of collecting complete clutches of eggs.

METHODS

Techniques for measuring eggshell thickness have been described by Anderson and Hickey (1970) and Ratcliffe (1970). We measured thickness using a modified Starrett Model 1010M thickness gauge, accurate to 0.01 mm. Three measurements were taken at different places around the blow-hole of each egg of the three nonpasserine species. Only those eggs with the blow-hole located near the "equator" were used. Eggs of the Mockingbird and Loggerhead Shrike are too small to measure thickness directly with the instrument described above. To estimate their thickness, the length and breadth of these eggshells were measured to the nearest 0.05 mm, using a vernier dial caliper

graduated in 0.05-mm intervals, and the shells were weighed to the nearest 0.01 g on a 100-g-capacity, top-loading, pan balance. These measurements were then used to calculate Ratcliffe's (1970) thickness index, a parameter closely correlated with actual thickness. We have endeavored to use only eggs that appeared clean inside and those with small blow-holes, in order to control weight variability.

Significant variation in eggshell thickness over broad geographic areas has been demonstrated for some species (Anderson and Hickey, 1970, 1972). Thus, for each species we have restricted our analysis to eggs collected in a relatively small region on the assumption that geographic variation is reduced to a trivial level. Black-crowned Night Heron eggs were from Massachusetts, Rhode Island, Connecticut, and extreme eastern New York. White Ibis and Loggerhead Shrike eggs were from Florida, Clapper Rail eggs from Virginia, and Mockingbird eggs from South Carolina and nearby Georgia. All of these eggs were collected between 1876 and 1943.

We assume that eggs in museum collections represent random samples from the given localities. We found no indication in the collections or in the field notes of the collectors that certain eggs were selected in preference to others, except that they usually tried to take fresh *first* clutches. All collectors probably attempted to obtain complete clutches. Their original field notes verify that complete clutches were selected after repeated visits to the nest or upon flushing a bird off the nest in species where incubation generally does not begin until the last egg is laid (Lloyd Kiff, pers. comm.). Collectors also accumulated or communicated knowledge of what a full clutch of eggs should be for the species. Thus, we believe that incomplete clutches were rarely taken, and that the inadvertent inclusion of a few of these clutches in our large samples does not significantly bias our data.

We assume that shell thickness remains essentially constant after an egg is collected and dried, that is, that the materials do not sublimate or otherwise decrease.

Statistical procedures follow those presented in Sokal and Rohlf (1969).

RESULTS AND DISCUSSION

Variability—Variation in shell thickness for each of the five species has been analyzed as a Model II (random) nested analysis of variance (anova), with unequal sample sizes (Table 1), using the clutch of eggs as the primary sampling unit. For the nonpasserine species, the procedure separates variation in thickness into three hierarchical levels: among clutches, among eggshells within clutches, and among measurements (error).

Variation in thickness of shell among clutches probably depends on: differences in the stages of incubation, differences related to clutch size, genetic and physiological differences between females, differences in diet among females within and between local populations, differences in gene pools between local populations, differences in environmental conditions between years, and other unknown factors (Kreitzer, 1972; Romanoff and Romanoff, 1949; Rothstein, 1972). Variation among eggs within clutches is probably due to day-to-day differences in calcium metabolism and eggshell deposition in individual females. The main factors which contribute to the among-measurements (error) mean square are: differences in eggshell thickness at the three

TABLE 1
NESTED ANALYSIS OF VARIANCE FOR EGGSHELL THICKNESS FOR FIVE SPECIES

| Species and Source of variation | Degrees of freedom (df) | Mean squares (MS) |
|--|-------------------------|-------------------|
| Black-crowned Night Heron ^a | | |
| Among clutches | 81 | .00423583* |
| Among eggs | 254 | .00048310* |
| Among measurements (error) | 672 | .00003343 |
| Total | 1007 | |
| White Ibis ^a | | |
| Among clutches | 193 | .00344592* |
| Among eggs | 407 | .00081443* |
| Among measurements (error) | 1202 | .00005435 |
| Total | 1802 | |
| Clapper Rail ^a | | |
| Among clutches | 59 | .00513168* |
| Among eggs | 466 | .00033180* |
| Among measurements (error) | 1052 | .00005133 |
| Total | 1577 | |
| Mockingbird ^b | | |
| Among clutches | 80 | .00489155* |
| Among eggs (error) | 231 | .00067398 |
| Total | 311 | |
| Loggerhead Shrike ^b | | |
| Among clutches | 72 | .00383473* |
| Among eggs (error) | 255 | .0043458 |
| Total | 327 | |

^a Based on three thickness measurements (mm) per egg.

^b Based on one thickness-index measurement per egg.

* $P < .001$

points of measurement, imperfections in the micrometer within the limits specified by the manufacturer, and human error in applying and reading the instrument.

An analysis of variance was performed on White Ibis data to test differences among nine localities in Florida. These differences were found to be non-significant ($P < .01$). We conclude that most of the variation among clutches is due to individual differences in females and possibly to yearly differences in environmental conditions.

In the Mockingbird and Loggerhead Shrike, we made only one determination of the thickness index for each egg. For this reason, variation due to the intrinsic inaccuracies in measuring and to other within-egg variables could

TABLE 2
STATISTICS OF EGGSHELL THICKNESS FOR FIVE SPECIES

| Items analyzed | Species Studied | | | | |
|------------------------------------|---|----------------------------|------------------------------|-------------------------------|-----------------------------------|
| | Black-crowned Night Heron ^a | White Ibis ^a | Clapper Rail ^a | Mocking- bird ^b | Loggerhead Shrike ^b |
| Variance | | | | | |
| Among clutches (s^2_c) | 0.0003055 | 0.0002832 | 0.0001829 | 0.0010949 | 0.0007567 |
| Among eggs (s^2_{egg}) | 0.0001499 | 0.0002533 | 0.0000935 | 0.0006740 | 0.0004346 |
| Among measurements (s^2) | 0.0000334 | 0.0000544 | 0.0000513 | — | — |
| Percent of the variability | | | | | |
| Among clutches | 62.50 | 47.93 | 55.81 | 61.90 | 63.52 |
| Among eggs | 30.66 | 42.87 | 28.52 | 38.10 | 36.48 |
| Among measurements | 6.84 | 9.20 | 15.66 | — | — |
| Overall mean thickness or index | 0.28348 | 0.34752 | 0.25792 | 0.54332 | 0.51506 |
| Number of clutches | 82 | 194 | 60 | 81 | 73 |
| Number of eggs | 336 | 601 | 526 | 312 | 328 |
| Clutch size | | | | | |
| Mean | 4.10 | 3.10 | 8.77 | 3.85 | 4.50 |
| Range | 2-7 | 1-5 | 4-12 | 2-5 | 2-6 |

^a Based on direct thickness measurements (mm).

^b Based on thickness-index measurements.

not be separated from variation among eggs within clutches. Thus, differences among eggs within clutches cannot be tested and the number of levels in the anova is reduced to two. The coefficients of variation for thickness index among eggs within clutches for these species are similar to those for shell thickness for the other three species.

Statistics derived from the anova are presented in Table 2. Variances have been calculated from expected mean squares. Variation at each level is also expressed as a percentage of the total variance. Most of the variation occurs among clutches, but a substantial proportion is found among eggs within clutches. The percentage of the variation occurring among measurements of the same egg is small.

Percentages of variation for groups and subgroups are fairly consistent from species to species. A notable exception is found in the White Ibis, in which the percentage of the total variation occurring among eggs within clutches was greater than for the other species. This finding is related, in part, to obvious differences in size and shape of eggs within clutches. Generally, eggs in clutches of other species were more uniform in these characteristics. Furthermore, because eggs of White Ibis are larger and have

thicker shells than the other four species considered here, there is greater opportunity for variability.

Complete clutches vs. one egg per clutch—To get at the question of whether to collect whole clutches or some fraction of each, we computed the *relative efficiency* (RE) of one design with respect to the other. RE is a ratio, usually expressed as a percentage, of the variances resulting from the two designs being compared. The appropriate formula as given in Sokal and Rohlf (1969:289) is

$$RE = \frac{s_{\bar{y}}^2 \text{ of design B}}{s_{\bar{y}}^2 \text{ of design A}} \times 100$$

where \bar{y} here represents the mean of a group of clutches. The expected variance among clutch means ($s_{\bar{y}}^2$) for each design can be derived from estimated variance components for each level in the nested analysis of variance (Table 2) according to the formula:

$$s_{\bar{y}}^2 = \frac{s^2}{mec} + \frac{s_{ECC}^2}{ec} + \frac{s_C^2}{c},$$

where s^2 , s_{ECC}^2 , and s_C^2 are the respective estimates of the variance among measurements within eggs, among eggs within clutches, and among clutches; and m is the number of measurements per egg, e the number of eggs sampled per clutch, and c the number of clutches sampled.

We computed estimated variances of \bar{y} for a theoretical design A in which the entire clutch is utilized and for a second design, B, in which the sampling unit is one egg selected randomly from each clutch. In design A, the number of eggs measured per clutch (e) has been determined as the whole number nearest to the mean clutch size for the respective species (see Table 2). In design B, $e = 1$. Values of $m = 3$ and $c = 10$ were constant for all calculations of $s_{\bar{y}}^2$ for Black-crowned Night Heron, White Ibis, and Clapper Rail. These values were selected because our empirical estimates of variances were based on three measurements per egg, and ten clutches approximate the required sample sizes estimated in the next section of this paper. The value $c = 10$ was also used for Mockingbird and Loggerhead Shrike, but $m = 1$. Thus, there is no estimate of s^2 within measurements and the formula is reduced to two components.

$$s_{\bar{y}}^2 = \frac{s_{ECC}^2}{ec} + \frac{s_C^2}{c}.$$

Table 3 shows the gain in efficiency of design A compared to design B. The relatively large differences in thickness observed among eggs within

TABLE 3
RELATIVE EFFICIENCY (RE) OF COLLECTING WHOLE CLUTCHES (DESIGN A) VERSUS
COLLECTING ONE EGG FROM A CLUTCH (DESIGN B)¹

| Species | Mean clutch size | $s_y^2 A$ | $s_y^2 B$ | $\frac{s_y^2 B}{s_y^2 A} \times 100$ | Increase in RE (%) of Design A over Design B |
|---------------------------|------------------|-----------|-----------|--------------------------------------|--|
| Black-crowned Night Heron | 4 | .3457283 | .4665033 | 134.9 | 35 |
| White Ibis | 3 | .3736778 | .5546333 | 148.4 | 48 |
| Clapper Rail | 9 | .1951889 | .2935000 | 150.4 | 50 |
| Mockingbird | 4 | .0001263 | .0001769 | 140.0 | 40 |
| Loggerhead Shrike | 5 | .0000844 | .0001191 | 141.2 | 41 |

¹ The number of measurements per egg and the number of clutches are constant in each design.

clutches (expressed as s_{ECC}^2 , see Table 2) contribute substantially to the sample variance (s_y^2).

In utilizing whole clutches, the investigator should be aware that inadvertent or intentional collection of a high proportion of incomplete clutches may bias the data, especially if sample sizes are small. Such conditions would occur if only the first one or two eggs of a clutch are collected and the shell thicknesses of successive eggs tend to differ from those of the first eggs. Thus, care should be taken to collect complete clutches. If partial clutches are collected the investigator should randomly choose the eggs.

Other designs could be compared in which the number of measurements per egg (m) or the number of clutches (c) would vary. However, variability between measurements (s^2) is small, and relative efficiency would be changed little by increasing the number of measurements per egg. If one wished to use one egg per clutch and still achieve a variance equivalent to that of design A, the percentage increase in the number of clutches to be sampled for each species would be approximately that shown in the last column in Table 2.

The relative efficiency of one design with respect to another is not very meaningful unless one considers the relative effort and time (or cost) involved in obtaining the data. Cost will vary greatly, depending on whether the species is abundant, whether colonial or solitary nester, how well it conceals its nest, and other characteristics. For most studies, the cost of removing the egg contents and measuring shell thickness is much less than that of finding sufficient nests and collecting the eggs. The investigator may also be confronted with a limited season in which eggs are available, extended travel cost and time, and other factors. Under such limitations, design A, which minimizes the number of clutches needed, will usually require the

least amount of time in the field. However, the total number of eggs to be measured is greater, as entire clutches are utilized.

The investigator must weigh the efficient utilization of time and resources against the impact on a species that collecting might have. Most species, except large birds of prey and albatrosses (which have long incubation periods), will lay replacement eggs when the entire clutch is taken or destroyed (Welty, 1962:295; Thompson, 1964:242). This trait was sometimes used by early oologists to get fresh eggs and/or increase their total take. Today, it might be used to minimize the impact of egg collecting. For instance, when the nests of a small proportion of breeding pairs are actually subject to the removal of the entire clutches, less disturbance occurs than when some fraction of the clutch is taken from a greater number of nests. Such disturbance, even though only one egg is taken, may also result in nest desertion by the birds.

Sample size estimates—After the sampling design has been selected, the investigator will want to know the number of clutches needed from each of “*a*” groups of nests in order to detect a minimum true difference, δ , in mean eggshell thickness. This assumes a probability, *P* (power), that the difference will be detected if it exists, and a probability, α , of incorrectly claiming a difference when none exists. Sokol and Rohlf (1969:247) present a relatively simple formula for estimating the sample size if one has a priori information of the sample variance. The formula (with *c* substituted for Sokol’s *n*) is as follows:

$$c \geq 2 \left(\frac{\sigma}{\delta} \right)^2 \{t_{\alpha[r]} + t_{2(1-P)[r]}\}^2,$$

where *c* = number of clutches, σ = true standard deviation for clutches, δ = the smallest true difference between means that one desires to detect, *r* = degrees of freedom of the sample standard deviation with *a* groups and *c* replications (clutches) per group, α = significance level, *P* = desired probability (power) that a difference will be found to be significant. Values of $t_{\alpha[r]}$ and $t_{2(1-P)[r]}$ are from a two-tailed *t*-table with *r* degrees of freedom, and probability levels of α and $2(1-P)$.

The sample estimate of the coefficient of variation (C.V.) and the percent difference between means that one wishes to detect can be substituted for σ and δ , respectively, because only the ratio of σ and δ are necessary, not their actual values. We computed estimates of sample sizes (number of clutches) needed to detect thickness differences (δ) of five and 10 percent (percentages arbitrarily selected) for each of the five species at significance levels of 0.05 and powers of 0.9 (Table 4). These estimates are based on a collecting

TABLE 4

ESTIMATES OF THE NUMBER OF CLUTCHES NEEDED FROM A LOCALITY TO SHOW DIFFERENCES (δ) IN THICKNESS OF EGGS¹

| Species | Coefficient of variation | Collecting Design | | | |
|---------------------------|--------------------------|-----------------------|------------------|----------------------|------------------|
| | | $\delta = 10$ percent | | $\delta = 5$ percent | |
| | | Whole clutches | One-egg clutches | Whole clutches | One-egg clutches |
| Black-crowned Night Heron | 6.55 | 11 | 15 | 38 | 51 |
| White Ibis | 5.54 | 8 | 12 | 27 | 40 |
| Clapper Rail | 5.42 | 8 | 12 | 26 | 39 |
| Mockingbird | 6.56 | 11 | 15 | 38 | 53 |
| Loggerhead Shrike | 5.67 | 8 | 11 | 28 | 40 |

¹ Significance level (α) of 0.05 and power (P) of 0.9.

design in which complete clutches are utilized and each egg is measured three times. The formula is very sensitive to changes in the ratio of (σ/δ). This accounts for the marked dissimilarity in numbers of sets required for detecting five and 10 percent differences.

The estimates of required sample sizes are based on estimates of the variance from relatively large samples of archival eggs. We believe these estimates are relatively precise, but they may also be conservative. For instance, we have assumed that variation has not increased in the post-DDT era. This assumption may not be valid, but we do not have sufficient samples of these five species at this time to analyze variation in such eggs. If recent eggs are sufficiently more variable in thickness, the sample sizes required would be somewhat larger.

Table 4 also presents estimated sample sizes for a one-egg-per-clutch collecting design. The number of clutches is increased by the difference in relative efficiency between the two designs.

SUMMARY

Measurements of shell thickness of the eggs of five species were subjected to nested analyses of variance. The analyses separated variation into two or three levels for which variances and percentages of the total variation were derived. The results show that differences among measurements of the same egg contribute little to the sample variance, whereas differences among eggs within clutches contribute nearly as much as differences among clutches. It is more efficient and less costly to collect entire clutches of eggs in most studies of shell thickness. Using entire clutches, sample sizes needed to detect differences of 10 percent in shell thickness (at given significance levels and power) were estimated to be eight to 11 clutches for the species studied. For differences of five percent, 26 to 38 clutches are required. Guidelines are presented which may assist other

workers in evaluating the efficiency of their sampling designs, and in estimating sample sizes for detecting differences in eggshell thickness in wild birds.

ACKNOWLEDGMENTS

We thank L. J. Blus, D. R. Clark, Jr., and L. F. Stickel for their advice and critical reading of the manuscript. Data presented in this paper could not have been obtained without the generous cooperation of curators and their assistants at the following museums and universities: American Museum of Natural History, Carnegie Museum, Clemson University—Department of Zoology, Florida State Museum, Harvard University—Museum of Comparative Zoology, University of Massachusetts—Department of Zoology, Ohio State University—Museum of Zoology, Philadelphia Academy of Sciences, Smithsonian Institution—U.S. National Museum of Natural History, and Yale University—Peabody Museum of Natural History.

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31 JANUARY 1974.

GENERAL NOTES

Stretch and Snap displays in the Great Egret.—Although ritualized reproductive displays have been described in detail for many species of herons, Meyerriecks (Puhl, Nuttall Ornithol. Club, No. 2, 1960) noted the apparent absence of Stretch and Snap displays in the Great Egret, *Casmerodius albus*. In a heronry on Phillips Island near Beaufort, North Carolina, I have seen both of these displays in this species. During March and April, 1971–1973, I observed more than 25 egrets performing Stretch and Snap displays. I made detailed qualitative records of frequency, duration and sequences of display components for 11 birds, the results of which are summarized here.

The Stretch display consisted of the following sequential events: (1) moderate to full erection of scapular plumes and lowering of the neck to a vertical position with the bill extended, followed by twig-grasping or tremble-shoving movements resembling nest-building activity; (2) raising and stretching the neck with bill pointing vertically; and (3) depressing the head toward the back as the heel joints were rapidly bent. Some variation both between and within individuals was noted in the performance of the display. For example, the vertical neck-lowering component at the beginning of the display was occasionally repeated several times, accompanied by rapid flexion of the heel joints. Less frequently, the sequence of movements of the display was abbreviated such that vertical neck-raising and head depression occurred in the absence of prior neck-lowering. The sequence of movements in the display could also be interrupted by preening of the outer primaries. Preening most frequently occurred following either neck-lowering or head depression. Fig. 1 shows the typical sequential components of the Stretch display.

The Snap display was less variable and consisted of the following sequential events: (1) full scapular plume erection and extension of the neck out and down, immediately followed by (2) erection of feathers of head and neck, and (3) flexion of the heel joints to lower the body to the perch or floor of the nest. Heel joint flexion was accompanied by a loud snapping together of the mandibles. Fig. 2 illustrates the typical components of the Snap display.

In such herons as *Ardea cinerea*, *A. herodias*, and *Butorides virescens*, the general features of the Stretch display are as follows:

1. The bird extends the neck vertically upward.
2. Then the neck is lowered until the occipital portion of the head almost touches the back.
3. The bird lowers its body to the floor of the nest.
4. Crest or crown feathers and scapular plumes are erected.

In those species, as in the Great Egret, the Snap display is slightly less complex than the Stretch:

1. The bird extends the head and neck fully forward and downward.
2. Crest and neck feathers are erected, the degree depending upon the species.
3. The mandibles are snapped together, making a sharp sound.

In the Great Egret the head and neck were lowered at the inception of both displays, but several important differences exist between the Stretch and Snap. First, the distinct click of the bill which accompanied the Snap display was not associated with the neck-lowering component of the Stretch display. Also, head and neck feathers were not erected during neck-lowering in Stretch display, but erection was always a component of a Snap performance. In addition, the neck was more fully extended in the Snap display.

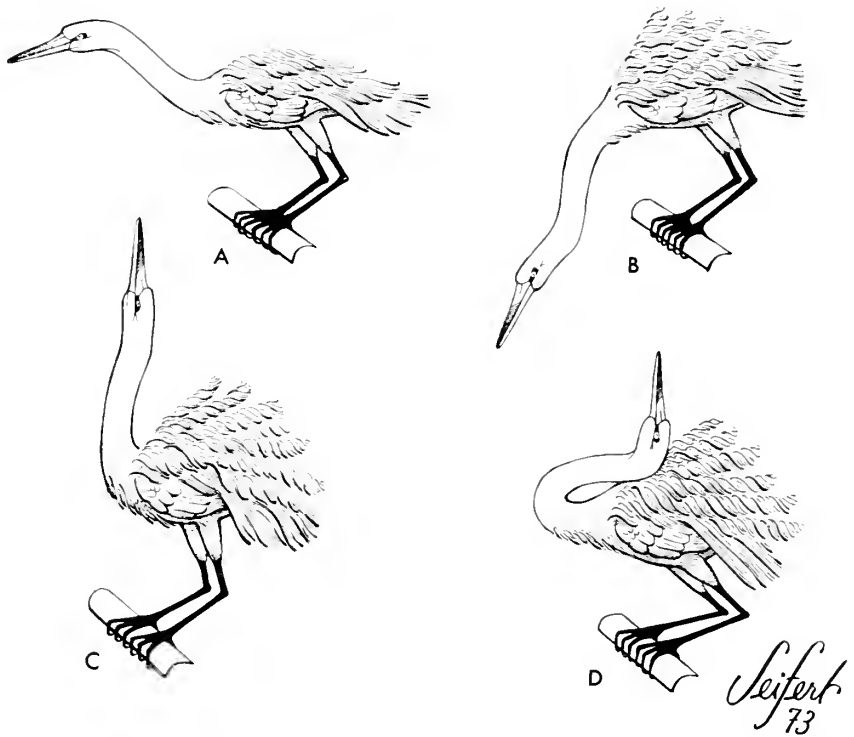


FIG. 1. Principal components of Great Egret Stretch display: From starting position (A), scapular plumes are erected as the bill is lowered (B) and then the head and neck are raised into a tightened "S" position (C and D) as the heel joints are bent.

Both displays occurred at the onset of the breeding season when displaying and nesting territories were being selected. All displaying birds had bright green lores and dark mandibles, characteristic of individuals of this species at the height of early breeding activity. Birds were not individually marked and the sexual monomorphism of this species precluded the positive identification of displaying individuals by sex.

The Stretch display definitely served to attract other birds of the species, and in two separate observations mounting of the displaying bird occurred. Thus, the display might be performed by both male and female Great Egrets. However, recent investigations of Cattle Egrets (*Bubulcus ibis*) suggest that females may mount in attempts to overcome the hostile tendencies of performing males (Lancaster, D. A., *Living Bird*, 9:167-194, 1970). The possibility exists, therefore, that the display may be performed exclusively by males. Obviously, both of these patterns reflect sexual drive. Meyerriecks (op. cit.) suggested that Snap displays are also indicative of hostile motives. However, further speculation would seem premature and in need of more detailed information on the displays.

I thank Jane Seifert for her excellent line drawings of the displays. Dr. B. S. Martof and Dr. T. L. Quay made helpful comments on the manuscript. These observations were

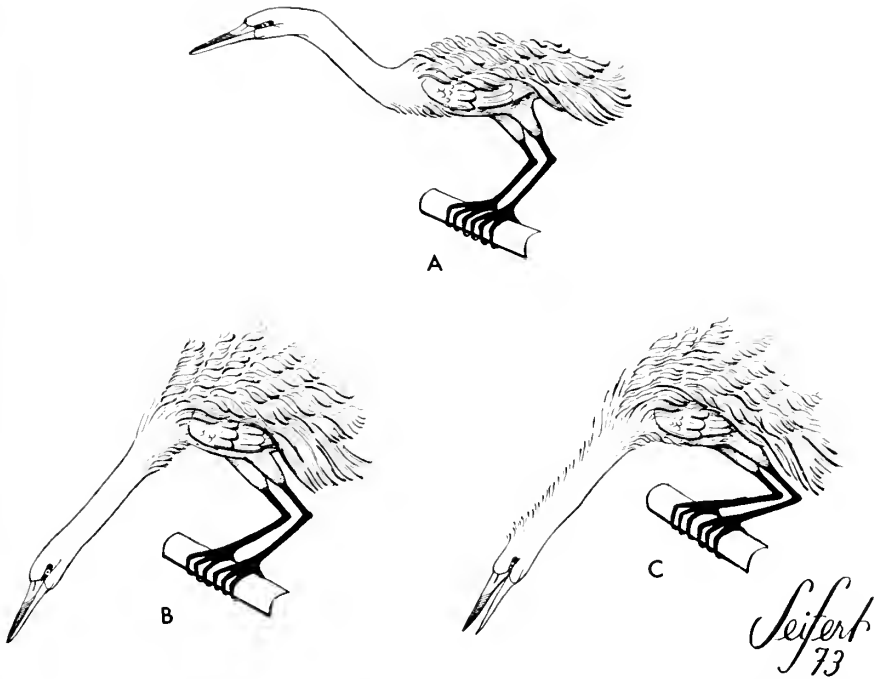


FIG. 2. Principal components of Great Egret Snap display. From starting position (A), scapular feathers are erected as the bill is lowered (B). The neck feathers are then erected, heel joints rapidly bent, and the mandibles snapped together (C).

made during the course of a study supported in part by grants from the Frank M. Chapman Fund of the American Museum of Natural History and the National Audubon Society.—DONALD A. MCCRIMMON, JR., *Department of Zoology, North Carolina State University, Raleigh, North Carolina 27607. Accepted 24 December 1973.*

Probable predation by Swainson's Hawks on swimming spadefoot toads.—Swainson's Hawk (*Buteo swainsoni*) captures both invertebrate and vertebrate prey, mainly insects and smaller mammals (Brown and Amadon, *Eagles, Hawks and Falcons of the World*, vol. 2, McGraw-Hill, New York, 1968; Bent, *Life Histories of North American Birds of Prey*, Part 1, Dover Publications, New York, 1961; Craighcad and Craighcad, *Hawks, Owls and Wildlife*, Dover Publications, New York, 1969). At least occasional captures are also made of birds and herptiles (McAtee, *Food habits of common hawks*, U.S. Dept. Agric. Circ. 370, 1935). All of these items are known to be taken on the ground or in the air. Our field observations show that flying *B. swainsoni* probably also captures adult plains spadefoot toads (*Scaphiopus bombifrons*) from the surface of open water.

Spadefoot toads are sporadic breeders, their appearance being dependent upon occasional heavy rains (Bragg, *Gnomes of the Night, the Spadefoot Toads*, Univ. Penn. Press, Philadelphia, 1965). Except for such normally brief periods, these animals are

relatively unavailable to avian predators. Two groups of chorusing spadefoots were observed from 16:00 to 17:00, on 12 June 1973, in a pond on each side of State Route 94, 0.5 km east of Punkin Center, Lincoln County, Colorado. This region is a shortgrass prairie now grazed by cattle. Chorus group 1 was in a temporary pond about 0.5 hectare in area and 1 m deep, and chorus group 2 in another such pond of about 1 hectare and over 1 m deep.

Our attention was first attracted to the toads by four Swainson's Hawks which were flying around the pond site of chorus group 1. The birds were obviously capturing some kind of prey, using two fishing techniques. One involved a slow, relatively shallow descent over the pond, extending the talons several cm into the water, picking up some small object, and flying off to land with it either on the shore or out on the prairie. The birds then proceeded to rip at the object and consume it. On one occasion, a hawk dropped into very shallow water and pummeled a prey item with its talons. We heard spadefoots calling at this site and suspected the hawks were capturing them. We investigated the ponds, causing the hawks to fly away; we could find no remains of the prey nor see toads in the water.

Chorus group 2 was then heard and we proceeded to it. There were seven *Buteo swainsoni* at this pond, fishing in the same two ways described earlier. The toads in this chorus group were clearly visible, floating in the middle of the pond as they called. The hawks were clearly seen to pick up and carry off toad-sized objects (five toads collected from pond 2 ranged in snout-vent length from 51 to 58 mm). Again, upon our approach the hawks flew away. We could find no remains of prey except for what was apparently a partly dried stomach of a toad-sized vertebrate.

While evidence that the hawks were capturing toads is largely circumstantial, our observations are strongly suggestive of this behavior. In addition, the ponds are temporary, hence, the hawks were not feeding on fish or some other aquatic prey. We also noted that adjacent ponds, which lacked chorusing toads, did not have hawks active around them.—OWEN J. SEXTON, *Department of Biology, Washington University, St. Louis, Missouri 63130*, and KEN R. MARION, *Department of Biology, University of Alabama, Birmingham, Alabama 35233*. Accepted 19 November 1973.

A specimen of *Larus glaucescens* from Hudson Bay.—On 1 June 1964 I collected a Glaucous-winged Gull (*Larus glaucescens*) from a flock of several hundred Herring (*L. argentatus*), Thayer's (*L. thayeri*), and a few Glaucous (*L. hyperboreus*) Gulls at a garbage dump at Fort Churchill, Manitoba. The specimen (Univ. of Michigan Museum of Zoology no. 211,531) is an immature female, apparently in second alternate plumage. Its measurements (in mm.) are: exposed culmen, 54.4; depths of bill at base, 18.2; depth of bill at gony., 19.3; wing (chord), 420; tail, 175; tarsus, 66.5. The weight was 1140 g, with little subcutaneous fat.

Because of the specimen's pale brownish primaries and rectrices, as well as geographic considerations and associated species, I originally identified it as an immature of *L. thayeri*. At that time I had had no prior experience with that species, the immature plumages of which have never been described in full.

The immature plumages of *L. glaucescens* are closely similar to those of *L. thayeri*, but the following characters allow the correct identification of the Fort Churchill specimen. One, the primaries and rectrices are pale grayish brown and essentially concolor with the wing coverts, mantle, and general body coloration; in *thayeri* the primaries are usually dark brown and contrast rather sharply with the mantle and body coloration.

Two, the rectrices, which are the same color as the primaries, are uniformly colored and lack any trace of mottling on the outer rectrix; in *thayeri* the rectrices are darker brown and the outer rectrix is mottled. Three, the wing coverts are finely dotted with white; in *thayeri* the edges of the wing coverts are deeply scalloped with white. Four, the specimen is too large for *thayeri*; its dimensions far exceed those given by Smith (Ornithol. Monogr., 4, tables 5 and 8, 1966) for a large series of female *thayeri* from the breeding grounds. On the other hand, it falls in the upper end or exceeds the dimensions of a small series of female *glaucescens* measured by Dwight (Bull. Amer. Mus. Nat. Hist., 52, 1925). Particularly evident is the specimen's heavy bill, which differs markedly from the shorter and slenderer bill of female *thayeri*.

In these and in other characters of plumage and soft part coloration, the Fort Churchill specimen is indistinguishable from *L. glaucescens*. There is no evidence of hybrid ancestry. At my request, Eugene Eisenmann and John Bull compared the specimen with the outstanding collection of larids in the American Museum of Natural History and independently reached the same conclusions.

The Glaucous-winged Gull is common along much of the west coast of Canada and the United States, but very rare away from the immediate vicinity of the Pacific. I know of only one seemingly unquestionable report from inland Canada, a bird banded as a chick in British Columbia and recovered in Alberta (Salt, Auk, 87:428, 1961; Merilees, Canad. Field-Nat., 75:170, 1961). Other Alberta records, the only other reports for interior Canada, (Salt, Canad. Field-Nat., 80:114, 1966; Stirling, Blue Jay, 25:131, 1967) lack details or measurements and are unconvincing.

Published specimen records for inland localities in the United States include Oklahoma (Sutton, Auk, 55:277-278, 1938), Arizona (Phillips, Marshall, and Monson, Birds of Arizona, Univ. of Arizona Press, Tucson, 1964), and California (McCaskie and Cardiff, Condor, 67:542-544, 1965). I have not examined these specimens. There are also sight records of *glaucescens* inland in several western states, e.g., Idaho (Burlleigh, Birds of Idaho, Caxton Printers Ltd., Caldwell, Idaho, 1972), but most of these lack any substantiation and the probability of confusion with *thayeri* is high. I have examined a recent specimen from Nevada that was thought to be *glaucescens* (Monson, American Birds 26:639, 1972), but it is clearly referable to *thayeri*.

Thayer's Gull winters commonly on the west coast and probably reaches its central arctic breeding grounds after an overland flight across western Canada and parts of the United States. Studies are beginning to indicate that this species occurs regularly in the interior. I suggest that the vast majority of records attributed to Glaucous-winged and Iceland (*L. glaucooides*) Gulls in the inland western United States and Canada are actually of Thayer's Gull. A full review of this subject, including examination of all alleged specimens, is needed.

I am indebted to Eugene Eisenmann and John Bull for their assistance and to W. Earl Godfrey for information on Canadian records of *glaucescens*.—JOSEPH R. JELL, JR., Natural History Museum, P. O. Box 1390, San Diego, California 92112. Accepted 11 February 1974.

First record of Sabine's Gull in Nevada.—On 21 September 1972, a Sabine's Gull (*Xema sabini*) was observed on Virginia Lake, a 40 acre impoundment in southwest Reno, Washoe County, Nevada. This constitutes the first verified sighting of a Sabine's Gull in Nevada. The bird, an apparent adult in nuptial (gray-headed) plumage, was first observed in the lake about 40 m offshore, where it fed in a dabbling manner for approxi-

mately one hour. Although California Gulls (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*) were present on the lake, the Sabine's Gull did not associate with them. During the next hour the bird was observed to fly around the lake several times after which it was not seen again. The characteristic triangular patches of black and white on the wings and the forked tail were easily seen as the bird flew; the light bill tip was also noted. Color photographs of the bird in flight and on the water were obtained and have been verified by Dr. Fred A. Ryser, Curator of Birds and Mammals, University of Nevada Museum of Biology. Copies are on file in the University of Nevada Museum of Biology, Reno, Nev. and in the U.S. National Photoduplicate File (accession number 62-1Ca.b) at Laurel, Md.—WILLIAM H. CLARK, 705 Smith St., Vale, Oregon 97918; KEITH I. GIEZENTANNER, Department of Game and Fish, Santa Fe, New Mexico 87501; and JAMES L. HAINLINE, Center for Water Resources Research, Desert Research Institute, Reno, Nevada 89507. Accepted 6 December 1973.

Unusual prey of Common Terns: swim-blisters of large fish.—While studying Common Terns (*Sterna hirundo*) in a large colony at Monomoy, Massachusetts, I saw on several occasions adult terns fly in with peculiar inflated objects and offer them to their chicks. During six days of observation between 14 and 31 July 1973, I saw at least 14 of these objects brought to a small plot containing 30 broods. A few others were seen being carried to other parts of the colony, and the total number brought into the colony of some 2000 pairs of terns must have run into scores, probably hundreds. Several were collected and were subsequently identified by Dr. R. H. Backus of Woods Hole Oceanographic Institution as swim-blisters of the common sea-robin (*Prionotus carolinus*).

The swim-bladder of this fish is a lung-shaped object consisting of a pair of inflated lobes, each about 40 mm long and 15–20 mm in diameter, joined together near one end and with muscles attached to the outer margins. In the live fish it occupies more than half of the visceral cavity. Illustrations of swim-blisters of this and related species are published in Damski et al. (Amer. Zool., 13:1147–1148, 1973), Tavolga (Nat. Hist., 69: 48–49, cover photograph, March, 1960), and Evans (Copeia, 1973:315–321, 1973).

The observation of terns carrying these swim-blisters poses two puzzles: how they obtained them and why they brought them to their young. The common sea-robin is abundant in the area, but is largely a bottom-dwelling fish and is larger than a tern, ranging to 400 mm in length and to 800 g in weight. It is inconceivable that a tern could catch one or extract the swim-bladder from a dead one. However, sea-robins are regarded as a nuisance by local fishermen and are often killed and discarded or cut up for bait. It is conceivable that as the body disintegrates or is eaten by scavengers, the swim-blisters would be released and float freely to the surface.

Even floating on the surface, this would be exceptional food for Common Terns, which feed almost exclusively on live prey. I have occasionally seen Arctic Terns (*S. paradisaea*) feeding on fish offal, but I have not previously identified such among several thousand items of food that I have seen fed to young Common Terns. Although Common Terns feed on a wide variety of invertebrates as well as on fish, these swim-blisters do not resemble any normal prey species, except perhaps inflated fry of the northern puffer (*Sphoerides maculatus*). I have never seen that species fed to the young, and indeed it would be dangerous to them (Porter, Audubon Mag., 1962:300–301). Furthermore, the bladders did not prove to be suitable prey, for the young could not swallow

them despite prolonged efforts. It is unusual for Common Terns to bring to their young food items that they themselves could not swallow, although they occasionally bring fish that are too wide or spiny for the young to swallow (Boecker, Vogelwelt, 89:221-225, 1968).

There was some evidence of a food scarcity at Monomoy at the time of these events. The amount of food brought by parent terns to chicks in my study-plot was generally less in late July than in early July 1973, and some chicks that had started to grow well declined and died late in the month. Hence, it is possible that the parents picked up the swim-bladders because they were unable to obtain suitable food. This proved to be a waste of time and effort by the terns, although at least one parent repeated the same behavior several times.

I thank R. H. Backus for his perspicacity in identifying the specimens. This is contribution no. 118 from the Scientific Staff, Massachusetts Audubon Society, and is part of a study supported by a grant from the Frederick W. Beinecke Fund.—I. C. T. NISBET, *Massachusetts Audubon Society, Lincoln, Massachusetts 01773. Accepted 30 January 1974.*

Monk Parakeets breeding in Buncombe County, North Carolina.—A native of South America, the Monk Parakeet (*Myiopsitta monachus*) has been imported in large numbers to the United States during the past decade for sale as a cage bird. Following accidental escape and intentional release, wild populations have become established in scattered localities, initially in New York and adjacent states (Bull. Linnaean Newsletter, Vol. 25, 1971; Briggs and Haugh, Kingbird, 23:3-13, 1973). Recent observations from Buncombe County, North Carolina indicate that a breeding population of Monk Parakeets is present in one of the interior river valleys of the southern Appalachian mountains.

Monk Parakeets were first reported in Buncombe County in May 1972, when several pairs were seen in West Asheville (elev. 2,200 ft.). Subsequently, numerous individuals, pairs, and large flocks have been observed in Enka (elev. 2,000 ft.), Asheville (elev. 2,100 ft.), Leicester (elev. 2,000 ft.), and Barnardville (elev. 2,200 ft.). Breeding pairs, with typical bulky nests located in silos and on utility or telephone poles, have been observed in Barnardville, with two nests in 1972 and two in 1973, and in West Asheville, with two nests in 1972 and one in 1973. Young were successfully fledged by at least three of the seven pairs, and photos of nests and adults have been sent to the National Photoduplicate File in Laurel, Maryland.

The increasing frequency of reports and evidence of successful nesting indicate that the species is presently well established in Buncombe County. There, the population is currently distributed within a 15-mile radius of Asheville, in the French Broad River valley and adjacent plateau, at elevations of 2,000 to 2,200 feet. This interior river basin is essentially separated from the adjacent piedmont and Appalachian Valley by mountain ranges of 3,500 to 6,000 feet in elevation, thus possibly restricting the movement of certain species into the region. Local pet store managers (pers. com.) in the Asheville area report selling Monk Parakeets during the 1960's and informed us of several incidents of accidental escape from private owners. These reports of escapes in this relatively isolated region suggest that the population is local in origin and not the result of an influx of parakeets dispersing from previously established concentrations elsewhere.

In addition to this large montane population, scattered sightings have been reported in 1973 from the piedmont and coastal plain of North Carolina. Donald T. Harke (pers. com.) of the U.S. Fish and Wildlife Service in Raleigh informs us of records from Statesville, Winston-Salem, Fayetteville, Greensboro, and Bladenboro; in addition, a specimen has been collected at Edenton and sent to the North Carolina State Museum in Raleigh. The occurrence of the Monk Parakeet across the three major physiographic regions of North Carolina is strong evidence for its ability to survive in the United States under a wide variety of climatic conditions, adding further concern over its potential impact on agriculture and the native avifauna.—MARCUS B. SIMPSON, JR., *Department of Pathology, Yale University School of Medicine, 310 Cedar Street, New Haven, Connecticut 06510* and ROBERT C. RUIZ, *300 Wilson Ave., Swannanoa, North Carolina 28778*. Accepted 14 December 1973.

Use of native plants by Monk Parakeets in New Jersey.—The Monk Parakeet (*Myiopsittus monachus*) has been classed a potential agricultural pest in the United States. This status is based on reports from its native Argentina, where it is said to destroy two to 45 percent of the crops within its range, preferring corn, sunflower, millet, sorghum and a variety of cultivated fruits (U.S. Dept. of Interior, Bureau of Sport Fisheries and Wildlife Leaflet, 496, 1971). In northeastern North America, where it is now considered a breeding bird, many have noted its dependence on the extensive network of winter bird feeders. The species also shows a fondness for cultivated grains and fruits at all seasons (Bull. Linnaean Soc. Newsletter, 25, 1971; Freeland, Wilson Bull., 85:332-334, 1973; Bull. Wilson Bull., 85:501-505, 1973; C. F. Leck pers. comm.); in one case, a single pair caused substantial damage in an apple orchard in Virginia.

The non-cultivated foods of the Monk Parakeet, in the U.S., are poorly known. Brief mention has been made of the species eating "berries," acorns, and the seeds of conifers and grasses (Bull. op. cit.; U.S.D.I. op. cit.). In March 1973, we discovered a pair of Monk Parakeets nesting in a park in Middlesex County, New Jersey. At that time of the year the area lacks cultivated crops and active bird feeders, so we felt that observation of the birds' food habits might be of interest. Consequently, we systematically observed the birds from 14 March until 28 April. They were not seen after the latter date, and we assume that they deserted the nesting area.

According to park employees, the birds had wintered in the area, when active feeders were available. When we found them, their activities were centered about a large stick nest. It had been built about 5 m from the ground in the characteristically-drooping lower branches of a large pin oak (*Quercus palustris*), located on a 600 m² island in a lake. The nest was large (about 0.125 m³) and constructed entirely of twigs, each about 50 cm long. Various plants were used in the nest, but they were mainly willows (*Salix* spp.) and oaks (*Quercus* spp.). A large portion of the birds' day was spent in nest repair. During our attendance they moved the tunnel entrance from the bottom to the side of the nest. The parakeets occupied a roughly square home range of approximately 120 hectares, including wooded areas (about 47 percent of the total area), lawns (25 percent), the lake (14 percent), and miscellaneous developed areas (14 percent).

In order to determine food preferences, we calculated the percentage of the observed foraging time (11 hours) that the birds fed on specific parts of various plant species. Identification of food items was aided by the parakeets' tameness, which al-

lowed very close observation. In order of descending preference, the food items were: buds of American elm, *Ulmus americanus*, (23 percent); berries of red cedar, *Juniperus virginiana*, (14 percent); seeds of white pine, *Pinus strobus*, (12 percent); acorns of pin oak (8.8 percent); buds of willows (7 percent); flowers of American elm (5 percent); fruits of American elm (5 percent); acorns of white oak, *Quercus alba*, (4.5 percent); buds of sweetgum, *Liquidambar styraciflua*, (3 percent); acorns of red oak, *Quercus rubra*, (2.3 percent); buds of red maple, *Acer rubrum*, (2 percent) and buds of fire cherry, *Prunus pensylvanica*, (2 percent). The remaining 11.4 percent consisted of unidentified food items.

Individual plants showed varied amounts of damage due to the parakeets' attention. Most individuals and species showed slight damage, but all the American elms in the area had the top one meter of their crowns completely stripped of buds, flowers, and fruits. Such trees presented a bizarre, scalped appearance when they leafed out. Most of the willows in the area also showed severe damage, probably the result of the birds' use of this group of plants as both food and nest material.

From our limited data, it seems likely that the Monk Parakeet deserves its current status as potential pest. If the pair we observed had not disappeared or had been part of the normal flock of 15-50 (U.S.D.I. op. cit.), damage to the park's vegetation would have been quite substantial.—WILLIAM M. SHIELDS, THOMAS C. GRUBB, JR. and ANTHONY TELIS, *Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903 (Present address TCG, Jr.: Department of Zoology, Ohio State University, Columbus, Ohio 43210). Accepted 22 January 1974.*

Evidence of the breeding of Saw-whet Owls in western North Carolina.—Pearson, Brimley, and Brimley (Birds of North Carolina, Bynum Printing Co., Raleigh, 1959) regarded the Saw-whet Owl (*Aegolius acadicus*) as a casual winter visitor to North Carolina, while the A. O. U. Checklist (Lord Baltimore Press, Baltimore, 1957) stated that the owl breeds "south [only] to central Ohio, West Virginia, and Maryland" in the eastern United States. Nevertheless, Stupka's (Migrant, 17:60-62, 1946) records of the Saw-whet Owl in the Great Smoky Mountains marked the beginning of a growing body of evidence, reviewed by Simpson (Chat, 32:83-89, 1968), that has established that the bird is regular in spring and summer in regions of suitable habitat in the mountains of western North Carolina and eastern Tennessee. Numerous records have been obtained there during the months of March through September, with reports coming from the Great Smoky, Roan, Pisgah Ridge, Black, Plott Balsam, and Great Balsam mountains. Within these ranges, records have been largely confined to elevations above 5,000 feet, in forests of Fraser fir (*Abies fraseri*) and red spruce (*Picea rubens*). These boreal forests reach their southern limit in the eastern United States at Tanasee Bald, Transylvania County, North Carolina, where frequent reports of Saw-whet Owls establish the species' presently known southern limit in the eastern United States during the breeding season.

Single Saw-whet Owls in the distinctive, chocolate-brown juvenal plumage have been reported in western North Carolina on four occasions, beginning in 1965. The first observation was by Peake (Chat, 29:110-111, 1965) on 10 July 1965, at 6,100 feet, on Richland Balsam in the Great Balsam Mountains, Jackson County. A. L. Schiffman (pers. com.) observed another on 1 September 1965, at 5,200 feet, on the southeast slope of Potato Knob in the Black Mountains, Buncombe County. Conley Moffett and Brad

Hawkins (Simpson, Chat, 36:39-47, 1972) captured a juvenile Saw-whet Owl in a mist net on 2 September 1965, at 5,800 feet, on Mt. Mitchell in the Black Mountains, Yancey County. The owl was banded and a documentary color photograph was sent to the National Photoduplicate File in Laurel, Maryland (accession no. 372-1T). Kenneth C. Parkes (pers. com.) has examined the photograph and reports that the bird is in the first prebasic (postjuvenile) molt, with the plumage indicating that the individual is a young of the year. The most recent sighting is that by Peter G. Range of a uniformly chocolate-brown juvenile on 2 September 1972, at 5,600 feet, on Devil's Courthouse in the Pisgah Ridge Mountains, Transylvania County. Devil's Courthouse is less than one mile northeast of Tanssee Bald and is the southernmost locality at which a juvenile has been reported in the North Carolina mountains.

Migration data from various localities in the eastern United States (Mueller and Berger, Bird-Banding, 38:120-125, 1967; Simpson, Chat, 32:83-89, 1968; Davis, Kingbird, 16, 1966) indicate that the earliest migratory movements of the Saw-whet Owl occur in late September and early October. The four records of individuals in juvenile plumage, all with dates at least one month prior to the species' known migratory period, combine with spring-summer records of adults to provide strong evidence that the Saw-whet Owl breeds south into the mountains of western North Carolina.—MARCUS B. SIMPSON, JR., *Department of Pathology, Yale University School of Medicine, 310 Cedar Street, New Haven, Connecticut 06510* and PETER G. RANGE, *514 Laurel Avenue, Johnson City, Tennessee 37601. Accepted 21 November 1973.*

Notes on asynchronous hatching and nestling mortality in White-necked Ravens.—Asynchronous hatching is a common characteristic of bird species with long nestling periods and unpredictable food supplies (Lack, Ibis, 89:302-305, 1947). Although most passerines have short nestling periods with synchronous hatching, many corvids, with their comparatively longer nestling periods, hatch asynchronously. In the British Isles, for example, all seven native corvid species are asynchronous in hatching (Lockie, Ibis, 97:341-369, 1955), as are Common Crows (*Corvus brachyrhynchos hesperis*) in California (Emlen, Bird-banding, 13:143-154, 1942). Recently, however, Davis and Griffing (New Mexico State University Agr. Exp. Sta. Res. Rep. No. 231, 1972) concluded that in White-necked Ravens (*Corvus cryptoleucus*), "hatching was nearly simultaneous." They examined 11 nests in May and June 1971, at approximately weekly intervals, and observed that newly hatched ravens from the same nest were usually of equivalent size. Contrary to their conclusions, I have found that White-necked Ravens hatch asynchronously.

In conjunction with physiological studies, I followed physical and behavioral development of nestlings in mesquite (*Prosopis juliflora*) communities in southern New Mexico, approximately 30 km west of Las Cruces. In the summers of 1972 and 1973, I studied seven raven nests containing eggs that hatched. These nests were visited each afternoon to record hatching of the eggs. Hatchlings were then tagged with color bands, which I replaced with larger sizes as the birds grew. I continued to visit nests, after hatching of the young, at least every other day for the first ten days and at intervals of less than five days after that. Birds were usually weighed, measured, and examined for developmental and behavioral changes at each visit. Nestling data pertinent to this discussion are summarized in Table 1. The interval between the hatching of the first and last nestling was three days for three nests, four days for three nests, and five days for one nest.

TABLE 1
SUMMARY OF WHITE-NECKED RAVEN NESTING DATA

| Nest number | Clutch size | Eggs hatched | Nestlings fledged | Dates hatched | Nestling mortality per date, with ages at death and causes ¹ |
|-------------|-------------|--------------|-------------------|---------------|---|
| I. | 4 | 4 | 0 | 2 June | 2 of 2 hatched, both 18 days (M) |
| | | | | 4 June | 1 of 1 hatched, 7 days (S) |
| | | | | 5 June | 1 of 1 hatched, 15 days (M) |
| II. | 5 | 4 | 0 | 15 June | 2 of 2 hatched, both 21 days (M) |
| | | | | 16 June | 1 of 1 hatched, 10 days (S) |
| | | | | 18 June | 1 of 1 hatched, 2 days (S) |
| III. | 6 | 5 | 4 | 25 June | none of 2 hatched |
| | | | | 26 June | none of 2 hatched |
| | | | | 27 June | 1 of 1 hatched, 3 days (S) |
| IV. | 6 | 5 | 3 | 26 May | none of 2 hatched |
| | | | | 27 May | none of 1 hatched |
| | | | | 29 May | 1 of 1 hatched, 2 days (S) |
| | | | | 30 May | 1 of 1 hatched, 1 day (S) |
| V. | 6 | 6 | 3 | 29 May | 1 of 3 hatched, 7 days (S) |
| | | | | 30 May | 1 of 2 hatched, 6 days (S) |
| | | | | 31 May | 1 of 1 hatched, 16 days (S) |
| VI. | 5 | 4 | 3 | 3 June | none of 2 hatched |
| | | | | 4 June | 1 of 1 hatched, 10 days (S) |
| | | | | 5 June | none of 1 hatched |
| VII. | 5 | 5 | 2 | 16 June | 2 of 3 hatched, 8 and 15 days (U) |
| | | | | 17 June | none of 1 hatched |
| | | | | 19 June | 1 of 1 hatched, 5 days (S) |

¹ Causes of mortality were: M = man; S = starvation; U = unknown.

Nest robbing by man and starvation accounted for most of the nestling mortality. Man was considered the cause of mortality if human and vehicle tracks were found leading to the nest site. The high human mortality factor may be partly attributed to the conspicuousness of ravens' nests and the fact that these nests were located near a populated area on public domain heavily used for recreation. Starvation was assessed as the cause of mortality if the nestling was not diseased, and if, for two or three observations preceding death, it showed abnormally low growth rates and developmental retardation.

Of the 11 nestlings assumed to have starved, eight died within the first eight-day interval, two at ten days, and one at 16 days (Table 1). This pattern, where most of the nestling mortality falls within the initial one-third of the nestling period, has been noted for Rooks (*Corvus frugilegus*) and Carrion Crows (*C. corone*) by Holyoak (Bird Study, 14:153-168, 1967). He suggested that this may be partially due to these species hunting for food farther afield than other British corvids, which have different nestling mortality patterns. Therefore, during the interval when most frequent feedings are required for the young, nestling mortality would be great. This explanation may also hold for White-necked Ravens which often forage at distances greater than 2 km from their nests (pers. obs.).

Ten of the eleven starved nestlings were either the youngest or next to youngest bird in the nest at the time of death (Table 1). This is similar to the situation in certain asynchronously-hatching raptors, in which the young that starve are the weakest and least able to compete for food.

As there were no traces in or around the nest of younger (ten days of age or less) nestlings that starved (or of unhatched eggs or eggshells), these were probably eaten or removed by the parents. The 16-day-old starved nestling remained in the bowl of the nest. Removing the younger dead nestlings but leaving older ones has also been observed for five corvid species in England (Holyoak, op. cit.).

Excluding clutches that failed completely, 86.7 percent of the eggs laid in 1972 hatched and 90.9 percent in 1973. Davis and Griffing (op. cit.) reported a hatch rate of 63 percent. This apparent discrepancy and their conclusion that White-necked Ravens hatch nearly simultaneously may be partly explained if they underestimated hatching rate and neglected early nestling mortality. Within the weekly interval between their observations the nestlings could have hatched over a three- or four-day period, one or two of the youngest could have died of starvation, and the parents could have disposed of the dead young, eggshells, and unhatched eggs. The remaining young would then be approximately the same size. The differences in hatching rates could possibly reflect adjustments to local or seasonal food supplies; however, this conclusion would be inappropriate in view of the small sample sizes.

I wish to thank Ralph J. Raitt and Walter G. Whitford for helpful criticisms of the manuscript.—RICHARD MISHAGA, *Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003, (Present address: Stone and Webster Engineering Corporation, Environmental Engineering Division, Boston, Massachusetts 02107.) Accepted 12 December 1973.*

Molt schedule of House Sparrows in northwestern Texas.—From January 1971 through July 1972, I collected House Sparrows (*Passer domesticus*) in Lubbock and Hockley Counties, Texas, as part of a study of the quill mite, *Syringophiloides minor* (Berlese). As examination for the mite involved individual removal of all primaries, primary coverts, secondaries, and rectrices, I routinely recorded data on molt status. Juvenile birds were determined by the degree of cranial ossification (Nero, Wilson Bull., 63:84-88, 1951).

Fifty-nine juveniles were collected in 1971. Molt was first noted in a bird collected on 4 August. Twelve juveniles taken during May (2), June (3), and July (7) had not begun molt. The height of the postjuvinal molt occurred in August and September, when 50 percent and 87.5 percent, respectively, of the birds were molting (Table 1). Greatest involvement of feather tracts occurred in September when 70 percent ($N = 7$) of the molting birds had simultaneous renewal of primaries, secondaries, and rectrices. The last juvenile to evidence molt was collected on 22 November.

Sixty juveniles were collected from April through July 1972. The single juvenile collected during April was not molting, but in May, six of eight juveniles collected were in molt—the first on 15 May. During June, 21 of 24 and in July, 22 of 27 birds evidenced molt.

A total of 130 adults was collected from July through November 1971. Eight of 11 females collected on 28 July were the first to evidence molt. These birds were collected at night from nests where they were either incubating eggs or brooding young. Primary one was in various stages of exsheathment on all birds.

TABLE I
MOLT SCHEDULE OF HOUSE SPARROWS DURING 1971

| | | No. of Birds Examined | Stages of molt in specimens | | |
|-------|-----------|-----------------------------|-----------------------------|---------------------|---------------------|
| | | | Molt not begun | Molt in progress | Molt com- pleted |
| July | Juveniles | 7 | 100% | — | — |
| | Adults | 38 | 79% | 21% | — |
| Aug. | Juveniles | 18 | 50% | 50% | — |
| | Adults | 23 | 30% | 70% | — |
| Sept. | Juveniles | 8 | 12.5% | 87.5% | — |
| | Adults | 31 | — | 97% | 3% |
| Oct. | Juveniles | 9 | — | 22% | 78% |
| | Adults | 21 | — | 70% | 30% |
| Nov. | Juveniles | 12 | — | 25% | 75% |
| | Adults | 17 | — | 18% | 82% |

The height of the postnuptial molt occurred in September when 97 percent of the birds examined were molting (Table I). The greatest involvement of feather tracts also occurred in September when all ($N = 30$) of the molting birds had simultaneous renewal of primaries, secondaries, and rectrices. The last adults to exhibit molt in 1971 were a male and female collected on 9 November.

During 1971 six adults were collected in which molt had stopped following replacement of primaries one and two. Four of these birds were caged for observation, and molt resumed in all after intervals of eight, 10, 16, and 47 days, respectively. This suggests that the birds had experienced molt suspension (King, Condor, 74:5-16, 1972) rather than arrested molt, where feather replacement is permanently stopped before completion.

I am grateful to Dr. M. K. Rylander for suggestions during the preparation of this manuscript.—STANLEY D. CASTO, *Department of Biology, Texas Tech University, Lubbock, Texas 79409. Accepted 30 November 1973.*

The question of possible surplus females in breeding Red-winged Blackbirds.—The Red-winged Blackbird (*Agelaius phoeniceus*) is a polygynous species, with each male having one to several females in his territory. Males holding territories appear to represent only a portion of those in the population, as Orians (Ecol. Monogr., 31: 285, 1951) found that their removal resulted in a replacement by other males in California. In females, Nero (Wilson Bull., 68:129, 1956) reported that within the territory of a male they hold their own subterritories in Wisconsin. This suggests that in a finite area, females compete for space, and thus a surplus might also exist of this sex. Brown (Wilson Bull., 81:293, 1969), however, has postulated that no such surplus exists, as the males should be able to accept all available females. To provide some insight on the question of possible surplus females in breeding populations, I have reviewed my data collected in connection with studies of reproductive behavior and physiology. The work was carried out near Waterloo, Nebraska, in 1968, with supplementary data obtained from post-breeding birds taken near Wooster and Vickery, Ohio, in 1967.

In 1968, earliest nests were found on 20 April, with the latest in late July. Table 1

TABLE 1
CHRONOLOGICAL RECORD OF ACTIVE NESTS AND FEMALES REMOVED FROM A BREEDING
POPULATION OF RED-WINGED BLACKBIRDS

| Date | Active nests | Females removed | Date | Active nests | Females removed |
|----------|-----------------|--------------------|---------|-----------------|--------------------|
| 25 April | 23 | | 30 May | 72 | 7 |
| 30 April | 36 | 3 | 5 June | 57 | 12 |
| 5 May | 78 | 4 | 10 June | 51 | 0 |
| 10 May | 105 | 3 | 15 June | 38 | 0 |
| 15 May | 119 | 3 | 20 June | 21 | 0 |
| 20 May | 102 | 9 | 25 June | 16 | 0 |
| 25 May | 80 | 6 | 30 June | 19 | 0 |

shows the number of active nests present between 25 April and 30 June. Very few (if any) females initiated nesting after 15 May, and all had begun nesting by 19 May, as evidenced by the unfeathered brood patches of nest-building birds (during construction of the first nest there are some feathers in the brood patch region). Every nest in the Nebraska study area was interrupted by me or by predators prior to the fledging of young. In some cases, I removed eggs and replaced them with artificial eggs to prolong incubation. In addition, 47 females were shot on the study area, 10 of these prior to 13 May when there was a peak of 123 active nests.

Between 15 May and 5 June, I removed 37 females, and 114 nests were interrupted. Over this period the number of active nests dropped from 119 to 57, a decrease of 62. Obviously, the shooting alone would not account for the decrease, as at most only 37 of the 62 deficit nests would have been so affected. The remaining decrease of 25 nests must represent birds that did not renest after their nests were interrupted. Possibly some of these interrupted birds waited longer to renest, as suggested by the fact that a decrease of only six nests occurred between 5 and 10 June—even though 12 females were shot during that period. However, even allowing for later nesting, the substance of these findings seems clear: the number of active nests found during the 1968 breeding season appears to have been the work of females that were either removed or had their earlier nests interrupted. In other words, no nests were found that seem to reflect the presence of a group of surplus females in the population studied.

Most of the females building first nests in mid-May were subadults. Such birds were distinguished from adult females on the basis of color of the upper lesser marginal coverts and the chin feathers, a method of determination which is similar to that of Payne (Univ. California Publ. Zool., 90:57-58, 1969). Overall, of the 56 females (all with brood patches) collected after nest-building began in 1968, 39 were adults and 17 subadults. Payne (op. cit.:50) reported that two of four first-year females taken in May and June had brood patches in his California studies. In Ohio in August 1967, I collected three females from flocks of post-breeding birds and live-trapped 22 other females for examination. Of these, 16 were adults and nine were subadults. All had recently nested, as indicated by the presence of brood patches. These data show that most (all in my study) females develop brood patches, including the first-year birds. If there were a surplus of females in a population, one would expect that more birds would lack brood patches—particularly the first-year females, which would probably form the bulk of any surplus.

On the basis of these findings, I suggest that most female Red-winged Blackbirds breed every year, with no notable surplus existing as non-breeding birds in a breeding population. Thus, the regulation of populations does not appear to be directly influenced by exclusion of potential breeders by territorial behavior of females.—LARRY C. HOLCOMB, *Department of Biology, Creighton University, Omaha, Nebraska 68178.*
Accepted 18 January 1974.

Vocal mimicry in the Violaceous Euphonia, *Euphonia violacea*.—In Trinidad, Violaceous Euphonias (*Euphonia violacea*) mimic many different species while singing. From June through September 1961, the last four months of my 3½ years residence, I

TABLE 1
SPECIES IMITATED BY *EUPHONIA VIOLACEA* IN TRINIDAD

| Species | Call imitated | Number of individuals mimicking call |
|--------------------------------|----------------------------|--------------------------------------|
| PSITTACIDAE | | |
| <i>Touit batavica</i> | flight call | 1 |
| CUCULIDAE | | |
| <i>Crotophaga ani</i> | alarm "aani" call | 1 |
| TROCHILIDAE | | |
| <i>Phaethornis guy</i> | "tich" flight call | 4 |
| DENDROCOLAPTIDAE | | |
| <i>Xiphorhynchus guttatus</i> | "kew" call | 1 |
| FORMICARIIDAE | | |
| <i>Formicarius analis</i> | "chook" alarm call | 2 |
| PIPRIDAE | | |
| <i>Manacus manacus</i> | "trrr" contact call | 2 |
| TYRANNIDAE | | |
| <i>Megarhynchus pitangua</i> | "klee lelele" | 3 |
| <i>Pitangus sulphuratus</i> | "kiskadee" | 1 |
| <i>Tolmomyias flaviventris</i> | "weet" | 1 |
| TROGLODYTIDAE | | |
| <i>Troglodytes musculus</i> | alarm call | 1 |
| TURDIDAE | | |
| <i>Turdus fumigatus</i> | "kikiki" alarm call | 3 |
| <i>Turdus nudigenis</i> | alarm mew | 3 |
| VIREONIDAE | | |
| <i>Hylophilus aurantifrons</i> | scolding tit-like note | 1 |
| THRAUPIDAE | | |
| <i>Tangara gyrola</i> | "tsee" contact call | 2 |
| <i>Ramphocelus carbo</i> | "chink" contact call | 2 |
| | squealing note when caught | 1 |
| <i>Habia rubica</i> | "pu pu pu" | 1 |
| <i>Tachyphonus rufus</i> | "chcck" | 1 |

made note of the content of all songs heard from this species. I identified the vocalizations of 17 species in 10 families as mimicked by the euphonias (Table 1). In their account of mimicry in the Violaceous Euphonia in Trinidad, Belcher and Smooker (Ibis, 79:532, 1937) reports imitations of only two species, the flycatchers, *Megarhynchus pitangua* and *Contopus cinereus*. All the imitations listed by me were heard in the Northern Range of Trinidad, mostly in the Arima valley. I also heard an adult male euphonia imitating the trill of the Tropical Kingbird (*Tyrannus melancholicus*) near Doctor's River in Tobago.

The euphonia's own song, often uttered without imitations, is a rapid warbling which includes rolling "chree" notes and is punctuated with occasional staccato "bee bee" calls. Imitations were inserted into this song and were perfect to my ear, except that they were much fainter when the model was a bigger species than the euphonia.

All mimicry heard was from adult males, except for two records of imitations by a bird in female-like plumage. This could have been a young male, as its imitations of the hummingbird, *Phaethornis guy*, and the thrush, *Turdus fumigatus*, were less expert than normal. One adult male imitated six different species in one bout of singing, and many imitated four or five species in a bout of song.

The euphonia probably learns the vocalizations of models living in its immediate vicinity. Thus an adult male that sang near an Indian settlement, with cultivation adjacent to forest, mimicked the Smooth-billed Ani (*Crotophaga ani*), the flycatchers *Megarhynchus pitangua* and *Pitangus sulphuratus*, and the thrush, *Turdus nudigenis*; all of these nested in the cleared land. Also imitated by this bird was the manakin, *Manacus manacus*, which nested in the nearby forest. Another adult male, singing in the entirely forested Cumaca valley, was heard imitating only *M. manacus* and *P. guy*, both forest species.

The most interesting piece of mimicry was heard from an adult male near our house; this was an imitation of the harsh squealing of the Silver-beaked Tanager (*Ramphocelus carbo*). This note is made when tanagers are captured, and between June 1958 and September 1961, 88 Silver-beaked Tanagers were caught in nets a few yards from the house; the majority of these squealed while being extracted from the net. At no other time did we hear this call from the Silver-beaked Tanager, but it is presumably normally uttered when the species is caught. Our activities evidently provided the euphonia with a unique opportunity to learn the call, which it must otherwise have little occasion to hear.

The situations in which a pure euphonia song and one including imitations are uttered appear not to be distinct. Songs with and without imitations were heard in the following situations: intermittently while feeding, from stationary birds by themselves, and during territorial border encounters—when two adult singing males come to within four or five yards of each other.

There are no published accounts of mimicking by other species of *Euphonia*, nor in *E. violacea* other than Belcher and Smooker (op. cit.). Slud (Bull. Amer. Mus. Nat. Hist., 128:345-349, 1964) describes vocalizations of a number of euphonias from Costa Rica as consisting of a wide repertoire of unmusical calls; it is probably a relatively short step from this situation to imitation of other species. Notably nearly all the calls imitated by the Violaceous Euphonia are rather unmusical and staccato, and many of them are alarm or contact calls.—BARBARA K. SNOW, *Old Forge, Wingrave, Aylesbury, Bucks, England*. Accepted 16 January 1974.

THE PRESIDENT'S PAGE

The expression "tempest in a teapot" is frequently used to describe an overreaction to an event of relatively minor importance. By this standard, the published and unpublished reactions among certain birders to the *32nd Supplement to the A.O.U. Check-list* (*Auk*, 90:411-419, 1973) might best be called a "hurricane in a thimble." Misconceptions or errors of fact about the *Supplement*, the *Check-list*, the A.O.U. Committee on Classification and Nomenclature, and, indeed, about the A.O.U. itself, have been perpetuated, all too often by people who should know better. I have a unique opportunity to serve in an interpretive capacity for bird students puzzled or misled by all of the brouhaha, in that I am both a member of the A.O.U. Committee that prepared the *Supplement*, and President of an ornithological society whose membership includes a large proportion of nonprofessional ornithologists.

Those of us who were around during the years 1944 through 1956, when a series of annual supplements in *The Auk* gradually transformed the taxonomy and nomenclature of the fourth (1931) edition of the *A.O.U. Check-list* into that of the fifth (1957) edition, can remember no such hubbub about the published changes, although there were far more of these (even, sometimes, in a single supplement) than were listed in 1973. This relative calm can no doubt be explained by the fact that in those years birding was still a recreation and not an organized cult.

The publicity given to the reactions of the more articulate (if not accurate) critics of the *32nd Supplement* culminated (or at least I hope it culminated) in the asinine and error-filled article, "The Busted Birds," in the 18 February 1974 issue of *Time* magazine. In this, an "infuriated enthusiast" identified only as a self-appointed spokesperson for the American Birding Association, described the dichotomy between that group and the A.O.U. Committee as one between "gung-ho list chasers" and "sedentary bathrobe birders." As most members of the Wilson Society know from field trips at meetings, many of the senior professional ornithologists are at least "gung-ho" birders, although seldom "list-chasers." But to describe the work of the A.O.U. Committee as that of "sedentary bathrobe birders" is only to use extreme language to verbalize a misconception that I have found also to exist among more level-headed but equally uninformed critics of the Committee.

There is an unfortunate impression extant that the Committee simply sits about in smoke-filled rooms and arbitrarily rules on the taxonomic or nomenclatorial status of North American species and subspecies of birds, almost (to listen to some of the critics) on an ad hoc basis, and *certainly* without any "field experience" with the birds involved. In point of fact, one of the ground rules of this Committee has always been that no decision to alter the taxonomic status of a bird or group of birds will be made by the Committee itself in the absence of *published information* supporting such a change. For this first of the post-1957 supplements, the Committee decided that it was not enough for a majority of the Committee *itself* to be persuaded of the correctness. State, Miss. 39762, will be the new editor of *The Wilson Bulletin*. His tenure starts that the changes would "conform to the treatment currently believed correct *by the great majority of active systematists*" [emphasis added]. And what kind of people are these active systematists? Museum fossils? Far from it. Examine the names of the authors whose papers are cited in support of taxonomic changes. Not all would call themselves systematists; not all, to be honest, are field men. But consider such names as Cooch, Dickerman, Dilger, Holmes, Jehl, McKinney, Meyerriecks, Phillips, Pitelka, Raitt, Short, N. G. Smith, Stein, and Sutton, among many others cited. These are men who *know* their birds, who have spent countless hours in blinds, or trudging through habitats ranging from bleak arctic islands to dense tropical forests, in pursuit of ornithological knowledge. When such men tell us, for example, that their studies

indicate that birds formerly thought to be different species will freely interbreed, or, conversely, that birds that appear to us to be virtually identical actually segregate out into two "kinds" that ignore each other as potential mates, I think the bird student who really wants to know more of the living world of ornithology will listen.

There is not space here to go into the emotionally-charged matter of the "official" English-language names applied to birds (which, contrary to general usage, are seldom either "common" or "vernacular" names). Nobody, least of all the members of the A.O.U. Committee (all of whom are or have been active birders) will deny the "gung-ho lister" the privilege of calling off as many ticks on his list as he likes, under whatever names he may choose. But this has nothing to do with the serious study of birds as living organisms, products of millions of years of evolution, and *that* is what most of us in both the American Ornithologists' Union and the Wilson Ornithological Society are concerned with.—KENNETH C. PARKES.

ORNITHOLOGICAL NEWS

AARON MOORE BAGG STUDENT MEMBERSHIP AWARDS

The preliminary announcement of the Aaron Moore Bagg Student Membership Awards (*Wilson Bulletin*, 85:490, 1973) stated that further details about these new awards would appear in the March 1974 issue of the *Bulletin*. No such additional information appeared in that issue, an oversight for which the President apologizes both to Mrs. Bagg, whose generosity has provided these awards in memory of her late husband, and to interested applicants. Final plans for the administration of the student membership awards will be made at the annual meeting in June 1974, and will be published later. Meanwhile, students may obtain information by writing to the Chairman of the Student Membership Committee, Dr. Douglas A. James, Division of Biomedical and Environmental Research, U.S. Atomic Energy Commission, Washington, D.C. 20545.

GEORGE MIKSCH SUTTON COLORPLATE FUND

Through an unfortunate misunderstanding, wording of the Council's announcement (*Wilson Bull.*, 85:456, 1973) of the George Miksch Sutton Colorplate Fund did not accurately represent Dr. Sutton's wishes in connection with contributions to this Fund. It is his desire that additions to the Fund that he created for the Wilson Ornithological Society, and that will bear his name, be obtained only through his own efforts. The Council is happy to honor his wishes. Former students and other friends of Dr. Sutton who may wish to contribute to the Society in some particular way to honor Dr. Sutton may do so, with his blessing, either by sending an unrestricted gift or by contributing to another of our special-purpose funds. The Council suggests the Louis Agassiz Fuertes Research Grant Fund, which was originally Dr. Sutton's concept, and which his gifts set into motion.

NEW EDITOR FOR THE WILSON BULLETIN

Dr. Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State, Miss. 39762, will be the new editor of *The Wilson Bulletin*. His tenure starts with the 1975 volume, preparations for which begin immediately. All new manuscripts submitted after 31 May 1974 should be sent to Dr. Jackson, as should any manuscript under revision sent in after 31 July 1974. If in doubt, authors are asked to send queries to Dr. Jackson—before sending in their manuscripts.

ORNITHOLOGICAL LITERATURE

AVIAN BIOLOGY, Volume II. Edited by Donald S. Farner and James R. King. Academic Press, New York and London, 1972:xxiii + 612 pp., many diagrams, charts, and photographs. \$34.00.—The second volume of this series covers several anatomical and physiological systems with the same high standards established in the initial volume. Topics covered are the integument, patterns of molt, control of molt, the blood vascular, respiratory, digestive, and excretory systems, nutrition, and intermediary metabolism. A sampling of these chapters shows that the individual authors and editors have maintained the general policy of presenting a “balanced account of avian biology at the beginning of the 1970’s.” Systematic and nomenclatural matters remain under the editorship of Kenneth Parkes and follow the same standards established in volume one.

The chapters are not designed to be encyclopedic treatments of each subject, but rather a discussion of important topics plus an introduction and guide to the literature. I examined each chapter with particular inquiries in mind, and felt that in most cases answers could be found in the cited references—if they were not available in the text itself. Areas of ignorance, however, are not always clearly pointed out. The chapters on nutrition and on intermediary metabolism are essentially treatises on the domestic chicken. This reflects the state of our knowledge of these aspects of avian biology and hopefully will stimulate comparative investigations of them. Nevertheless, these chapters are of less direct usefulness to ornithologists than the other chapters.

Peter Stettenheim’s excellent chapter on the integument is overshadowed by the superb monograph, previously written by Lucas and Stettenheim on the same subject (cited in the bibliography). The discussion of the avian lung/air sac system and mechanism of breathing must be reassessed in light of the recent monograph on this subject by H.R. Duncker (*Ergebn. Anat. Entwickl.*, 45, 1971); unfortunately Duncker’s papers appeared too late to be included in the bibliography.

I would like to emphasize the value of this volume in obtaining information and literature references on subjects that seem unrelated to the chapter titles. I found a good discussion of Herbst’s corpuscles and a reference to staining methods for elastic fibers, both topics of immediate interest to me, in unexpected places. Hence, this book should be perused carefully, even if one is not interested at the moment in the subject matter of the individual chapters.

The main handicap of this volume is its cost, which may well place it beyond the reach of many ornithologists. Yet, *Avian Biology* will be a valuable reference work for any serious student of birds; in spite of the expense of the entire set, I recommend strongly that it be given high priority in the book budget of every ornithologist.—WALTER J. BOCK.

AVIFAUNA OF THE EASTERN HIGHLANDS OF NEW GUINEA. By Jared M. Diamond. Publications of the Nuttall Ornithological Club, No. 12, Cambridge, Mass. 1972: vii + 438 pp., 42 figs., 19 tables, and 4 maps. \$15.00. (Obtainable from the Nuttall Ornithological Club, c/o Museum of Comparative Zoology, Harvard Univ., Cambridge, Mass. 02138.)—This monograph is one of the most important contributions to knowledge of New Guinean birds in the past several decades. Although incorporating data from avifauna papers published on the eastern highlands since the World War II, the treatise

is based mainly on original work carried out on two expeditions in the Karimui and Okapa areas south and east of Goroka in 1964 and 1966. Information presented deals with a summary of Diamond's and other previous ornithological explorations in the region; and an in-depth discussion of the distribution patterns, ecological characteristics, altitudinal distribution, zoogeographical relationships of the regional avifauna, the composition of the forest, non-forest, and non-breeding migrant bird faunas, and the environment and breeding seasons. An extensive annotated list is provided of all species recorded, covering taxonomic affinities, breeding, ecological distribution, voice, native name, and details of specimens collected.

The great strengths of this monograph are its thoughtful and provocative views on the evolution of distribution patterns and subspecies and species groups in the New Guinean highlands, its clear and often original account of ecological sorting mechanisms operating for montane birds in the region, and its wealth of field information on all species recorded. Diamond's theory of speciation in montane New Guinea invokes sequences of historic population disjunctions, recontact of populations, competition and extinction of one competitive form by another. In explaining the patchiness of distribution—one of the most disconcerting phenomena of the New Guinean avifauna—the author also has new and well-reasoned ideas. However, these may not necessarily apply generally to all montane populations, the disjunctions of some of which may merely reflect success or failure in recolonizing mountain massifs during periods of altitudinal life-zone expansion in Pleistocene times.

The account of ecological sorting mechanisms is well-contrived, for it comprehensively covers spatial aspects (altitude, habitat, vertical distribution within the forest stratum, and allopatry), food and foraging differences, and temporal (seasonal) segregation. Such studies are obviously the author's forte: his elucidation of correlations between the age structure of montane populations and altitude is new knowledge. The striking and varied effects of altitude on the distribution of the avifauna are strongly emphasized, justifiably so. Limits and transitions in altitudinal distribution are interpreted in terms of inter-specific competition. Unfortunately, the historic significance of concomitant vegetation transitions is not fully appreciated here. The fact is that the primary limits and transitions in bird distribution, graphically shown on the diagrams on pages 58-65, do coincide at 3800-4500 feet with a marked floristic (if not structural) change in rain forests throughout New Guinea. In this broad correlation between the altitudinal ranges of birds and vegetation, interspecific competition merely sharpens the transitions for birds.

Much of the field data gathered concerns feeding behavior and calls. The accounts of calls are the most carefully documented and comprehensive available for New Guinean birds.

While it may seem petty to single out shortcomings and misjudgements, attention should be drawn to some of them. Occasionally poor, even misleading examples are chosen to illustrate important principles and patterns of evolution, distribution and ecological segregation. Thus altitudinally allopatric forms such as the *Paradisaea raggiana* group—*P. rudolphi* and *Toxorhamphus novaeguineae*—*T. poliopterus* are used to illustrate east-west geographical allopatry. Elsewhere, lowland taxa have been used as examples to show differential rates of reproductive and ecological isolation in a quite inapplicable montane context.

There also seems at times a slight tendency to twist the facts to suit the argument. In an explanation of how species may be represented by different races on northern and southern scarps of the eastern highlands region, *Melanocharis striativentris* is given

as an example. This species is nevertheless monotypic in the region. Altitudinal replacement between species of the genera *Peneothello*, *Pachycephalopsis*, and *Poecilodryas*, implying exploitation of equivalent niches, is just not true in the simplified way it has been described. Members of these genera overlap altitudinally much more widely than Diamond suspects, exploiting subtly different forest niches and levels close to the forest floor. Nor can it be claimed, as has been, without evidence, that *Gerygone cinerea* and *Acanthiza murina* occupy the same niches and replace each other altitudinally. Species of the two genera always occupy different niches wherever they come in contact in Australia. In such cases—there are others as well—it seems that too many conclusions have been jumped to too quickly.

The area chosen for study under the heading of "Eastern Highlands" is partly incongruous, in that it includes the Lake Kutubu area on a lowland plateau that is well-isolated from the main eastern highlands region. This lowland avifauna has no real relevance to that of the eastern highlands. Its excision would have led to a tauter treatise and perhaps elimination of the extensive discussions of evolution and distribution in both lowland and montane faunas that stray beyond the essential scope of the work. By contrast, the annotated account of the species concentrates on the birds of Karimui rather than those of the Eastern Highlands as a whole. Published data from other areas are blended in rather perfunctorily and given prominence only where records from Karimui and Okapa are minimal or lacking. It is also inappropriate that much information on the food of species of "Eastern Highlands" birds is incorporated from geographically extraneous sources.

There are some wrong statements. The melanistic morph of *Accipiter novae-hollandiae* is not new to science, having been previously recorded from western New Guinea, and the call described for *Ptiloris magnificus*, actually a harsh bi-syllabic growl, is surely inaccurate. The taxonomic account of *Meliphaga flaviventer* is confused and poorly done throughout. *M. f. giullianetti*, recorded from Lake Kutubu and elsewhere in the eastern highlands, is not included under representative races; and the referral of the Karimui population to the Weyland Mountains race *rubiensis* is incongruous, as there are intervening forms.

Perhaps the most critical objection can be levelled at the generic treatment of the birds-of-paradise, the Paradisaeidae. Such a major revision as attempted here deserves to be based on original investigation and new data. It derives instead from a somewhat flung-together rehash of what has already been known about the family for the last decade or more; generic limits are no better based than those in the widely accepted treatments of Mayr and Gilliard, which used the same information. Diamond has embarked on a wholesale lumping of genera, recognizing only ten as compared with twenty by Mayr and Gilliard. To be sure, some lumping is overdue, such as *Drepanornis* with *Epimachus*, *Diphyllodes* with *Cicinnurus*, and *Phonygammus* with *Manucodia*. But the union of such structurally and behaviorally diverse groups as *Parotia*, *Astrapia*, *Cicinnurus*, *Seleucidis* and *Pteridophora* in the one genus *Lophorina* serves only to cloud relationships between them and obscure the still incompletely understood lines of evolution in paradisaeids as a whole. One serious nomenclatural error has slipped through as a consequence of the lumping: two different species bear the name *Lophorina magnifica*.

English vernacular names are given to all species. These are drawn from various sources and so contribute to the perplexing plethora of vernaculars presently in use for New Guinean birds. The need for standardization is now greater than ever.

The monograph is well-bound and printed in the high standards of the Nuttall

Ornithological Club. Unfortunately some misprints and gaps in cross-references have crept in, probably during the proof-reading stage.—RICHARD SCHODDE.

SURVIVAL STUDIES OF BANDED BIRDS. By Joseph J. Hickey. Special Scientific Report—Wildlife No. 15. Fish and Wildlife Service, U.S. Dept. Interior, Washington, D.C., 1952, reprinted with minor corrections 1972: 177 pp., 71 tables, 21 figs., paperbound. Price not given.—The original edition of this pioneer work was never reviewed in *The Wilson Bulletin*. It is still of interest from several points of view, and the Fish and Wildlife Service has made a useful contribution to modern libraries by reprinting it. This report discusses at length a methodology for analyzing banding data, with particular emphasis on the many inherent biases in these figures (some of which have since been corrected by the present day automatic data processing techniques used in the Bird Banding Laboratory, but many others of which are inescapable). By use of life tables, Hickey analyzes the population dynamics of ten species of North American birds, from cormorants to jays, with particular emphasis on the Mallard. He also provides for modern workers a base study of population dynamics before pesticides entered our environment. The research was conducted in 1946–47, but was almost entirely based on data gathered in the late 1920's through the 1930's; the report includes literature references through 1951. This study should be required reading for anyone embarking on an analysis of banding data.—MARY H. CLENCH.

THE WORLD OF THE WOOD DUCK. By F. Eugene Hester and Jack Dermid. J. B. Lippincott Co., Philadelphia and New York, 1973: 160 pp., 80 photos, \$5.95.—Because it is a game bird of widespread breeding distribution in the United States and because of the accessibility of its nests, the Wood Duck is among the more researched species of birds. Consequently much information on the species is available. In this book, Hester and Dermid have done a creditable job of assembling this information and making it available to popular readers. Much of the information came from their nearly twenty years of observations, but research reports by other workers have also been used, 60 references being listed in the bibliography.

The fine photographs of Wood Ducks and their habitat or animal associates make this an attractive book and provide a welcome supplement to the word descriptions. However, it is to be regretted that a natural-color illustration of a pair of Wood Ducks was not included. Black and white photographs and a word description (with a confession of its inadequacy) are poor substitutes for a natural-color illustration of the male of this species.

The authors' experience with their subject and familiarity with the literature enabled them to write a book providing little chance for argument. However, there are several items with which I disagree. Hester and Dermid state (p. 73) that a "place" (presumably a water area) of at least 10 acres is essential for use by a Wood Duck brood. At the Olentangy Wildlife Experimental Station in Ohio, I found as many as five broods gathering on and successfully using ponds of less than half this size. Also, I found Wood Ducks feeding only in the mornings and evenings of autumn, whereas Hester and Dermid say that the birds spend the day feeding at this season (p. 93).

Certain areas of the Wood Duck's world are covered more satisfactorily than others, perhaps reflecting the thrust of the authors' research. For example, northward movement after the nesting season, as shown by band recoveries, is not mentioned although it occurs among Wood Ducks the same as other ducks.

I find it most unfortunate that a book in Lippincott's Living World Series has been written to promote hunting interests (p. 114), for the time has come when sport hunting must go the way of market hunting. With human population steadily increasing and wildlife habitat diminishing, sport hunting simply must be phased out, and this can best be done by discouraging our young people from engaging in it. To justify sport hunting, Hester and Dermid use the worn-out rationalization that hunters kill only birds that would otherwise die from natural causes. Actually, the size of the Wood Duck population is probably now limited chiefly by shooting, with a scarcity of safe nesting cavities a secondary factor. During the winter of 1972-73, I placed 30 Wood Duck nest boxes on 14 beaver ponds in north-central North Carolina, and only one of these boxes was used by nesting Wood Ducks. This low rate of usage could have resulted only from a scarcity of Wood Ducks. Hester and Dermid note (p. 44) that shooting may sometimes eliminate local breeding populations. While the desire of hunters to have Wood Ducks to shoot has provided motivation for helping Wood Ducks, I dream of a day when help to Wood Ducks will not come left-handedly.—PAUL A. STEWART.

THE WORLD OF THE RUFFED GROUSE. By Leonard Lee Rue III. J. B. Lippincott Co., Philadelphia, 1973: 160 pp., 86 photos. \$5.95.—The Ruffed Grouse has been the subject of two major treatises (Bump et al. 1947; Edminister, 1947); in Rue's book, this grouse is again given monographic treatment. As in the earlier accounts, the species is discussed in a New England context. Whereas the former two publications were essentially scientific documents, written by and for wildlife managers, Rue's book is a popular account, written largely from the natural historian-sportsman's point of view and presumably directed at readers with similar interests.

The book is divided into four sections: Characteristics, Annual Cycle, Relationships with Man, and Nomenclature of Ruffed Grouse. Unhappily it is neither as authoritative nor as accurate as its predecessors, albeit somewhat easier to read. For serious students of avian biology this book will be a great disappointment. The text is marred by categorical statements for which there is no scientific evidence, and inaccuracies for which there is no excuse. The photographic record, which includes 86 black and white photographs, is also much below the standard expected in popular publications in 1973.

Throughout the text, Rue's bias as a hunter shows in his obvious interest in the exceptional rather than the average bird (largest size, greatest weight, record crop volume, greatest distance travelled, oldest bird, etc.), and in the pages devoted to appropriate gear and dogs for hunting this species.

In discussing the characteristics of Ruffed Grouse, Rue deals with a spectrum of attributes, from external and internal morphology to population phenomena. Unfortunately, in discussing these attributes he often ignores important considerations. For example, in treating sexual dimorphism in plumage, he seems unaware of changes in mensural characters with the first postnuptial molt. The photograph on page 26 purports to show the difference in the rectrices of males and females; however, it fails to show the feature referred to, namely the incomplete bar in the tail (cf. photograph on page 16). In fact, the illustration would be a more appropriate example of differences in shape and size of tails of yearling and adult birds. The discussion of color phases in Ruffed Grouse leaves the reader with the impression that two distinct forms exist—red and grey phases. Certainly in the central part of the bird's range, every intermediate gradation imaginable exists.

The author's understanding of such physiological attributes as digestion in Ruffed Grouse seems superficial at best. He states (p. 38): "the crop . . . is used as a storage compartment, corresponding to the rumen of a deer. It serves the same purpose, allowing the bird to feed quickly and then digest its food at leisure." The crop, unlike the rumen, allows food to bypass until the rest of the gut fills; there is no evidence that digestion occurs within it. In discussing the passage of food through the gut, Rue states (p. 39): "From the gizzard, food passes through the duodenal loop and the large and small intestines." In using large and small, Rue is either confused about the passage of food or referring to lengths rather than diameters, a procedure not generally followed in anatomical descriptions.

With reference to population phenomena, Rue states (p. 39): "The Ruffed Grouse population is also controlled by a ten-year cycle, so that the population fluctuates widely from year to year and area to area." The first part of the statement tells us nothing. What population is Rue referring to—spring or autumn? How can a population be controlled by a ten-year cycle? The last part of the statement does not follow, because if population abundance of this species follows a cyclical curve, the widest fluctuations will not be from year to year but will be several years apart. The reader's understanding of causes of changes in abundance of Ruffed Grouse is not clarified by statements which seemingly contradict the above, for example, on page 74, "adverse weather [in summer] is probably the most important factor controlling the population." Yet on page 131, the author claims "overwinter mortality usually runs to 70 percent of the grouse's autumnal population," implying that winter is the most significant period because it "is a time of testing" (p. 115).

Rue's discussion of territoriality in Ruffed Grouse leaves one confused. He states (p. 44) that young birds, being less dominant, acquire less desirable territories, yet he states that only eight percent of territory holders move to new territories. What happens to these young birds when they become adults? Is the mortality rate on "desirable" territories only eight percent and on "undesirable" territories near 100 percent? How are these figures reconciled with a 70 percent overwinter mortality (p. 131)?

Inconsistencies in the text do not enhance the credibility of the author. On page 44, Rue states that "the environment will not support (or the grouse themselves tolerate) more than four males per square mile in spring." Yet on page 141 one reads "one grouse to four acres of land is considered maximum carrying capacity for the best of habitat, because the grouse themselves will not tolerate a higher population," presumably in autumn. Assuming an equal sex ratio, which is reasonable if one accepts the contention that the species is monogamous (p. 59), then by my calculations each hen would have to produce 28 chicks to reach such densities. This is four times the number Rue states survive to the end of the summer (p. 91). Another example of such inconsistencies is the average weight of males—20 ounces on page 20 and 23.3 ounces on page 99. On page 69, an interesting anecdote appears: "after a week or so of brooding her eggs, [the female Ruffed Grouse] will discard any that are infertile by rolling them out of the nest." One wonders what the selective advantage of such a behavioural pattern might be and how often this has been documented.

Inaccurate statements in the text are inexcusable. For example, Rue maintains (p. 72) that at hatching "ten primary and fifteen to seventeen secondary feathers show as small, dark, wet strings." Bump et al. (1947) showed 26 years ago that only 7 primaries and 9 secondaries were visible at hatching. Rue also maintains (p. 102) that "all of their [adults'] primary feathers will have blood in the shaft until the end of the year," imply-

ing that molting continues until the end of December. I know of no data supporting such a contention, and my experience has been that even the most distal primary in adults is bloodless by the middle of October.

The quality of the photographs suffers on two counts—technical flaws and poor subject matter. With the present high level of technological sophistication in photography, there is really no excuse for out-of-focus photographs (pp. 19, 25, 40, 56, 107, 109, 147), ones that have been obviously retouched (pp. 21, 30, 33, 107), or that fail to show what is indicated (pp. 26, 29). Excepting the pictures of shot birds, nearly all Rue's photographs fail to show the Ruffed Grouse to any advantage. The dishevelled state of the plumage and the fact that many pictures show the same bird and background suggest to me that the author has used captive birds for most of his pictures.

It is interesting that Rue refers to the A.O.U. Check-list (1957) in connection with the subspecies of Ruffed Grouse, yet he does not follow it when naming other species. Thus, the Rock Ptarmigan (*Lagopus mutus*) is referred to as *Lagopus rupestris* (p. 35), and Franklin's Grouse (*Canachites canadensis franklinii*), as *Canachites franklini* (p. 21). The photograph labelled Franklin's Grouse is, in fact, a female Blue Grouse (*Dendragapus obscurus*).

In conclusion, although this book contains a great deal of information on a popular species of game bird, it is badly marred by unsubstantiated anecdotes, informational inconsistencies and inaccuracies, and poor quality photographs.—D. A. BOAG.

ALBERTA VIREOS AND WOOD WARBLERS. By W. Ray Salt. Publ. No. 3 Provincial Museum and Archives of Alberta, 1973:121 pp., 9 col. pls. by Ludo C. E. Bogaert. Paper cover. \$4.50. (Obtainable from Provincial Museum and Archives of Alberta Bookshop, Edmonton).—When the author of this publication was engaged in writing *The Birds of Alberta* (W. R. Salt and A. L. Wilk, 1958, revised 1966, Department of Industry and Development, Edmonton, 511 pp.) he became increasingly aware of a considerable body of relevant information that was of necessity excluded from the book. The present volume, the first of a proposed series, makes available in detail much of that excluded information dealing with the status of 30 (two of hypothetical status) wood warblers and four vireos in Alberta.

Each species account opens with a brief version of the derivation of the vernacular and scientific names. Distribution within the province is carefully deduced from a presentation of thoroughly-compiled supporting data. Distribution of the subspecies, as well as the species, within Alberta is included. A section on nesting and its aspects includes valuable information on habitat, timing, nest site, nest materials, clutch size, cowbird parasitism, and song. Migration within the province is dealt with in considerable detail, with early dates of arrival and late dates of departure for various Alberta localities.

The data are, in general, abundantly documented as is attested by a 4½ page bibliography and a list of 24 sources of previously unpublished information. However, the citations of (Young, 1922) and (Clarke, 1939), on page 37, are not included in either list. (Young, 1922) apparently refers to C. H. Young's field notes made between May 15 and September 22, 1922, in Waterton Lakes Park, Alberta, and (Clarke, 1939) evidently to Dr. C. H. D. Clarke's notes made in 1939, also in Waterton Lakes Park, and compiled by Wildlife Division, National Parks Bureau, Ottawa, pp. 1-18.

Autumn plumages of the warblers and vireos are depicted in color as an aid to the identification of these birds in their more difficult fall aspects.

This publication will of course be especially useful in Alberta, but its carefully compiled data on nesting and habitat are often hard to come by and will be useful also to anyone who may need to compare these local data in connection with studies of geographic variation in aspects of reproductive cycles. This attractive and informative publication is a bargain at the price asked.—W. EARL GODFREY.

GROUSE AND QUAILS OF NORTH AMERICA. By Paul A. Johnsgard. University of Nebraska Press, Lincoln, Nebraska, 1973:xx + 553 pp., col. paintings by C. G. Pritchard, J. P. O'Neill, D. F. Landau, and L. A. Fuertes. \$25.00.—The literature on game birds in North America is remarkably rich, both in monographs dealing with individual species and in shorter journal publications and bulletins. It is a formidable task to master this literature and put it together in a concise form. Dr. Paul Johnsgard has done this remarkably well. His objective was to produce a dual-purpose volume, of value both as a reference work for the biologist and as a source book for the naturalist and hunter. On the whole I think the author has achieved his objective.

The book contains nine chapters in Part I dealing with comparative biology and 23 chapters in Part II, each of which deals with a species. There are keys to identification of adults (only) which are easy for the layman to follow, as good diagrams of body regions and feather areas are provided at the beginning of the book.

Many who are not linguistic scholars will be interested in the short section on name derivations. New to me was the revelation that the origin of the name *Colinus* is from a Nahuatl (e.g. Aztec) root.

One of the two indices is based only on vernacular names of species and a second on scientific names. Categories such as molt, food, distribution, eggs, etc., are not listed. If the book is to be used as a reference work, it is not sufficient to know that the California Quail is mentioned on 79 different pages. Even the Table of Contents does not help, as it does not give the pages on which the various sections within chapters appear. The absence of a good general index is a serious deficiency.

The value of Part I, the more technical section of the book, lies in the literature summaries and the opportunity to make comparisons quickly among species.

Chapters are provided on Evolution and Taxonomy, Physical Characteristics, Molts and Plumages, Hybridization, Reproductive Biology, Population Ecology and Dynamics, Social Behaviour and Vocalizations, Aviculture and Propagation, and Hunting Recreation and Conservation.

I did not like a few generalizations. For example, "Most quail and grouse are fairly mobile, but few undertake true migrations" (p. 82) is a statement inconsistent, as far as grouse are concerned, with the chapters dealing with individual species. Migratory populations exist or have existed in all North American species of grouse except the Ruffed Grouse. Accounts of migration of Spruce Grouse have not yet been published, but there is reason to believe that a migratory population of Spruce Grouse exists in northwestern Ontario and northeastern Manitoba. In Eurasia most of the grouse species have at least one migratory population. The ability to migrate, so widespread among the grouse, is at variance with what we see in most other galliform groups. It deserves to be stressed and examined in detail. In contrast, among the American quail only the Mountain seems to have migratory populations.

The chapter dealing with social behavior and vocalizations contains useful speculation about the evolution of strong pair bonds in the quails and the virtual disappearance

of territorial behavior in some species. This is contrasted with the grouse subfamily in which territoriality is unusually well-developed.

The evolution of lek behavior after the emancipation of males from nest guarding and brood care duties, and through the presumed greater attractiveness to females of groups of displaying males, has also been suggested by Snow (1963) in regard to manakins.

I agree with Johnsgard on the likelihood that the Sage Grouse, the prairie grouse group, and the Black Grouse of Eurasia evolved their lek behavior independently.

The descriptions of the postures and movements that compose quail displays are not up to the standards set for grouse. For example, the tidbitting display of the Bobwhite is mentioned without a description of the postures. On the other hand, treatment of quail calls is much more thorough than that of the grouse.

The taxonomic arrangement followed for the grouse is that of Short (1967), whose work was based on literature review and the study of museum skins. While I think that the arrangement is basically correct and a great improvement on previous classifications, a study of morphology alone can be misleading.

Aldrich and Duval (1955) were the first to treat the Lesser Prairie Chicken as a race of *Tympanuchus cupido*. Short (1967) judged as trivial many of the differences between Greater and Lesser Prairie Chickens cited by Jones (1964) to justify specific status for the latter. Johnsgard has followed Short in his treatment of the Lesser Prairie Chicken. Anyone who has seen both the Greater and the Lesser Prairie Chickens on their leks cannot but be impressed by the differences in the sounds they produce. The "gobbling" calls of the Lesser Prairie Chicken can be distinguished from the booming notes of its larger relative as far away as they can be heard. Indeed there seems to be a greater similarity, but not homology, with some of the calls of the Sharptail Grouse than with the Greater Prairie Chicken. There are other behavioral differences that seem to me to be greater than one would expect of a race. For example, Lesser males duet, a behavior that is never seen in the Greater Prairie Chicken. I would be most interested to know the function of these distinctive differences if they do not serve the purposes of species identification, advertisement, and isolation. Johnsgard elsewhere agrees with Sharpe's (1968) suggestion that the Lesser Prairie Chicken should be treated as an allospecies, but because this view has not received general acceptance, in this volume he has treated the Lesser Prairie Chicken as a subspecies.

The discussion of the evolution and relationships among the ptarmigan is sometimes inconsistent and, with respect to the White-tailed Ptarmigan, hard to accept. Morphologically this species would seem to provide a link between the *Dendragapus* grouse group and the Rock and the Willow Ptarmigan. The eggs of the White-tailed Ptarmigan are sometimes indistinguishable from those of the Spruce Grouse, and differ from those of the Rock and the Willow Ptarmigan. Beneath the feathering on the toes the White-tail has well-developed pectinations. These structures appear in greatly reduced form on the terminal joint only of the toes of the Rock Ptarmigan but are virtually absent in the Willow Ptarmigan. It seems likely that alpine-tundra floras evolved on the tops of the Rocky Mountain chain as it was pushed up during the Tertiary, perhaps before tundra appeared in our present arctic. The high level of endemism in the alpine-arctic flora of the British Columbia-Yukon-Alaska area suggests that this was a center of evolution for this vegetation. It seems likely that the White-tailed Ptarmigan is the closest living relative of an ancestral ptarmigan that evolved with this flora. Invasion of the arctic could have given rise to the Rock Ptarmigan and, eventually, the Willow Ptarmigan.

Polygamous or promiscuous mating habits predominate among the grouse. There is no reason to presume that monogamy was the ancestral or more generalized type of reproductive behavior for grouse. The ptarmigan and perhaps the Hazel Grouse seem to be the only species in which partial monogamy is present. The Willow Ptarmigan, in which pair bonds are stronger than in the other ptarmigan species, would seem to be at the end of an evolutionary trend rather than "primitive" as suggested by Johnsgard. Even in the Willow Ptarmigan, the nature of the monogamy recorded differs from that observed in, for example, many passeriform or anseriform genera.

I could find no mention of the distinctive nature of the juvenal plumage in the ptarmigans. All three species are set apart from the rest of the grouse by the absence of central white shaft streaks on much of the dorsal plumage and by the presence of white spots on the tips of the feathers—these giving a spangled appearance to their backs.

It is hard for this reviewer to accept eastern Asia as the area of origin for the Spruce Grouse and Sharp-winged Grouse. Behavioral evidence suggests that the Spruce Grouse is closer to the ancestral stem of the family than any other living species. Within *Dendragapus*, behavioral elements are relatively simple in the Spruce Grouse and become more complex and elaborate in the Blue Grouse. Finally, they become very complex in the Sage Grouse and there may even be grounds for merging *Centrocercus* with *Dendragapus*. It is likely that the Sharp-winged Grouse was a late Tertiary invader of Asia that did not succeed in penetrating far into the continent because of canalization of its gene pool.

The book contains many illustrations in color and black-and-white, the standard of which is somewhat variable. The 28 color photographs of the grouse are excellent, but their value could have been enhanced with better captions. The only information given is the species and sex of the bird depicted. Some of the black-and-white photographs of grouse are very good, particularly the action shots of Greater and Lesser Prairie Chickens fighting. Some add nothing to the beautiful color photographs and others are either badly reproduced, or the originals were not really of publication quality (e.g., some of the ptarmigan pictures).

Most of the color photographs of quail and the Grey Partridge are not up to the standard of the grouse color photographs but are, nevertheless, good illustrations. This is perhaps excusable, as wild quail are far more secretive and harder to waylay for photography in their native habitats than are grouse. The tropical forest species indeed must be almost impossible to photograph in their native range. To overcome this deficiency, nine color paintings of quails by Pritchard, O'Neill, and Landau are reproduced. The hitherto unpublished study by Fuertes of the hybrid Scaled \times Gambel's Quail is, in my opinion, a gem.

Of the 28 black-and-white photographs of quail and the Chukar, 18 are of birds in captive settings: these may be good illustrative material but I find them unaesthetic.

Two photographs show the cloud forest habitat of the Buffy-crowned Tree Quail and the Spotted Wood Quail. The only other quail habitat photograph is of the tropical rain forest habitat of the Singing Quail. I would have welcomed more photographs of the habitats of the less well-known neotropical quails.

Two plates by Pritchard show the downy young of grouse and quails. Contrast in the down patterns in all these paintings seems to me to be overaccentuated. I have never seen a Ruffed Grouse chick as dark in color as the one depicted. The few Sage Grouse chicks that I have seen have a most unusual brown and black spectacle mark on the lower neck. This mark seems to cover the area where the green gular skin patches

will eventually develop. This diagnostic mark is not illustrated or mentioned in the text.

The numerous black and white figures and diagrams are of high quality and make their points. Distribution maps are often extremely difficult to produce in such a way that all are satisfied. Range expansions or contractions often go unrecorded for many years in the literature; an author cannot be expected to know about all of them, but he is sometimes unfairly faulted for not recording them. A species, the range of which has changed over a period of time, is particularly hard to illustrate. The prairie chickens are a case in point. The Greater Prairie Chicken's original distribution has been described in the text. The boundaries of its expanded range, coincident with early farming methods, have been indicated by a dashed line, and its present distribution is indicated by shading. Yet there are late 19th century published accounts (McIlwraith 1894) of prairie chickens living in Ontario 100 miles east of the boundary indicated.

The range of the Bobwhite Quail in Ontario has greatly contracted from the extensive range indicated. Clarke (1954) was apparently the authority for this distribution, but his range map has not been followed by Johnsgard. There have been no self-sustaining wild populations on the north shore of Lake Ontario for 70 years.

Johnsgard has made an excellent digest of the existing literature, but except for some of the information on the quails, his book contains little that is new. Interested laymen will find much to stretch their horizons, for the book is well-written and is never boring. Professionals will find it a useful book for teaching and reference, and will probably feel that it is not overpriced at \$25.00, considering current prices. If a second revised edition is contemplated, a good index will raise its value greatly.—HARRY G. LUMSDEN.

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BEHAVIOR, MIMETIC SONGS AND SONG DIALECTS, AND RELATIONSHIPS OF THE PARASITIC INDIGOBIRDS (*VIDUA*) OF AFRICA. By Robert B. Payne. Ornithological Monographs No. 11, American Ornithologists' Union, 1973:vi + 333 pp., photographs, maps, audio-spectrographs, paper cover. \$8.00 (\$6.40 to A.O.U. members).—This important study deals with a group of small African birds that have long baffled museum taxonomists. Parasitic indigobirds have variously been treated as comprising from a single, polymorphic, polytypic species to as many as eight distinct specific taxa. Because of the great similarity in morphological (plumage) characters, and the impossibility of ascer-

taining from museum specimens which females belong with which males, these small birds were the despair of those, including this reviewer, who had occasion to write about them. The relationships that might be postulated between them defied adequate definition in the usual terminology of avian taxonomy, either of the old typological, or the newer biological, species concept.

Over many years it was learned through the piecing together of observational data, largely fragmentary and anecdotal individually, that the indigobirds are parasitic in their breeding, using firefinches (*Lagonosticta* spp.) as their hosts. In 1929, Neunzig first brought out evidence of unusual mimicry, largely buccal, between the nestlings of the parasites and of their hosts. His presentation suffered from lack of sufficient recorded data, and gave the appearance of circular reasoning, i.e. if the mouth-markings of a nestling indigobird closely resembled those of the young of a given species of firefinch, it was advanced that it was parasitic on the latter to the exclusion of other possible hosts, but to which it seemed less similar.

With the advent of sound recording techniques and the use of audiospectrographs, which made possible objective, direct comparisons of the songs of the species of hosts and of parasites and which eliminated the hitherto difficult personal factor of the investigator's auditory acuity, Nicolai was able to show close vocal mimicry to be of primary importance in the host-parasite relationships of these birds. Nicolai advanced the argument that speciation in the indigobirds was a result of host-specific imprinting—as evidenced by the evolutionary development of buccal characters and song imitation, rather than a result of geographical or ecological isolation. It was to test this thesis that Payne made the very meticulous and extensive field observations, with sophisticated techniques, such as playback experiments, reported in the present work.

Indigobirds present innumerable difficulties to the investigator of their breeding biology. They are promiscuously polygynous; they form no pair bonds; the females go to their host nests without the males—to which they were attracted selectively in the first place by their specific vocal mimicry of definite host species. In addition to their mimetic songs, the indigobirds also have complex non-mimetic vocalisms, often involving an extensive repertoire. Payne found that in some areas of Africa two or more kinds of indigobirds live together without interbreeding while in other areas “every species of indigobird appears to interbreed with another kind.”

On the whole, Payne's conclusions, fortified with ample and excellent data, corroborate and extend Nicolai's earlier ones. For the first time we now are given evidence from the biology of the living birds—as contrasted with the earlier mute evidence of their plumage characters, that makes possible a solution of the complicated relationships of these creatures. Payne recognizes four species with numerous subspecies. At the same time, he admits that many of the central African specimens in museums remain unidentifiable, and writes that “the pattern of morphological variation in the complex will remain enigmatic at least until tape recordings are made and singing birds have been collected in the Congo.”

Payne's book is of great interest, not only in its elucidation of an exceedingly puzzling group of birds, but also in pointing out a mode of speciation direction otherwise unknown in our understanding of avian systematics. It still remains to be seen what, if any, changes in the picture and in his interpretation of it, may result from his further field studies after the book was published.—HERBERT FRIEDMANN.

THE NATURAL HISTORY OF GARDNER PINNACLES, NORTHWESTERN HAWAIIAN ISLANDS. By Roger B. Clapp and THE NATURAL HISTORY OF KURE ATOLL, NORTHWESTERN HAWAIIAN ISLANDS. By Paul W. Woodward. Atoll Res. Bull. Nos. 163 and 164, Smithsonian Institution, Washington, D.C., 1972:iv + 25 pp. and xxi + 318 pp., maps, charts, photos. Prices not given.—The purposes of these reports are to bring together the all-too-brief and scattered information in the literature and in unpublished manuscripts, to present a short history of early exploration and biological activity (up to the early 1960's), and to record the current status of the vertebrate fauna and the vascular flora of certain Hawaiian islands, as observed by the Pacific Ocean Biological Survey Program of the Smithsonian Institution.

The historical narrative includes brief remarks on the ships that touched, and sometimes wrecked, on these land masses, along with some of the biological observations of the visitors. The sections on the vegetation are brief. Both studies provide information on climatic and general conditions and geology, but the data for Gardner Pinnacles are very limited, as might be expected from the extremely small land area (about eight acres) and from the few short visits that have been made to these precipitous, bare rocks.

The major emphasis is on the avifauna, while fish are not mentioned. Two species of sea turtles and two of geckos are indicated to occur, as are the Polynesian Rat (*Rattus exulans*) and the Hawaiian Monk Seal (*Monachus schauinslandi*), two whales, two dolphins, the ever-present domestic dogs, a monkey and domestic pig. The latter two, fortunately, are gone.

Each report contains a seemingly comprehensive section on literature pertinent to these land masses. However, many references pertinent to the observations in the species accounts are not included.

There is real value in gathering old knowledge of such isolated bits of land and in bringing forth new information, no matter how fragmentary. The ecosystems represented are little known and deserve far more attention than has previously been accorded them. Hopefully, some studies included in the International Biological Year will give further impetus.

The following comments apply primarily to Woodward's Kure Atoll study, which lasted more than five years and covered more than 2,300 man-days on the atoll. This one-sided attention of my review in no way disparages the worth of the limited data presented on Gardner Pinnacles.

In my opinion, the most important contributions concern the breeding biology of species of seabirds on Kure, especially their seasonality, numbers, and inter-island movements. The information on total estimated numbers in the populations, on numbers of "non-breeders," or numbers of casualties is only of limited value until we also know the ages, sexes, and biological states of the individuals included. Much the same can be said for the data on the recapture rates of birds banded without knowledge of these parameters.

Very useful for easy comparative study are the generalized graphs depicting cycles in breeding and in populations (pp. 69-71), the table of egg dates in various years (pp. 72-75), and the inter-island movements of banded birds (pp. 84-86).

The more extensive, and generally more valuable, species accounts are those of the Bonin Petrel, Wedge-tailed Shearwater, Christmas Shearwater, Red-tailed Tropicbird, Blue-faced Booby, Brown Booby, Red-footed Booby, Great Frigatebird, Sooty Tern, Gray-backed Tern, Brown Noddy, Black Noddy, and White Tern. Of less merit are the accounts of the Black-footed and the Laysan Albatrosses, perhaps because they

seem largely to duplicate (though generally support) studies on nearby Midway Atoll, or perhaps simply because I am more familiar with the biology of these two species.

The importance of long-term studies in bringing to light additional problems or in calling attention to new areas of information is evident in several of the accounts. For example, in some species, population estimates vary near 100 percent for comparable two-week periods in successive years. This can be seen in the Wedge-tailed Shearwater (p. 123), the Red-tailed Tropicbird (p. 136), the Red-footed Booby (p. 187), and the Great Frigatebird (p. 207). These variations do not appear to be parts of trends in population numbers, as is evident for the Sooty Tern (p. 247). What is their origin? Are they evidence of cyclic breeding, of changes in food supply, of disturbance? Or of differences in the techniques and dispositions of the estimators? Why do some other breeding species (e.g. Blue-faced Booby, p. 150) fail to show short-term swings in numbers? What is responsible for the fluctuations in the numbers of certain migrants—American Golden Plovers or Ruddy Turnstones?

What are the factors causing the irregular variations in egg dates, demonstrated for the Red-footed Booby (p. 195), Brown Booby (p. 173), and Red-tailed Tropicbird (p. 139)? Why, in 1966, did the Blue-faced Boobies (p. 156) delay egg-laying until March, when they initiated it in January or early February in the other five years of observation?

In summary, the authors and their co-workers have provided major additions to our knowledge and in many cases have furnished a basis for evaluating certain features of biological change. They are to be commended.

Having said this, I venture a critical comment. I hope that the authors and editors of future reports in this series will reduce the repetition of information in text, tables, and charts; that they will eliminate as far as possible information already established and published; that they will more thoroughly integrate the new information with that previously known (*cf.* most species accounts); and that they will eliminate irrelevant material (e.g. numbers of birds "handled," birds banded, or collected, and the amount of time spent, person by person).

Such "derelictions" probably came about through attempts to produce a complete picture of the islands and of the energy expenditures by the observers. But omitting them will make the worthwhile information, so abundantly present in these papers, more readily and pleasantly apparent to the reader, and will reduce the feeling, engendered particularly by the lengthy paper on Kure Atoll, that these are really "in-house" reports.—HARVEY I. FISHER.

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Madagascar Crested Ibis,
Lophotibis cristata,
Ankarafantsika Reserve.



Closeup of the same ibis,
showing lowered crest.
Photographs by Frank B. Gill.

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THE MADAGASCAR CRESTED IBIS, A THREATENED SPECIES IN AN ENDEMIC AND ENDANGERED AVIFAUNA

G. STUART KEITH, A. D. FORBES-WATSON, AND D. A. TURNER

The Madagascar Crested Ibis (*Lophotibis cristata*) occurs both in the humid forest of the east and the dry forest of the west in the Malagasy Republic (formerly Madagascar). Rand (Bull. Amer. Mus. Nat. Hist., 72: 143-499, 1936) found the bird common 40 years ago, but in our experience in 1972 it was distinctly uncommon. Thus it may already be declining in numbers, and certainly it is threatened by the destruction of its forest habitat. This is a handsome ibis with a large crest, and wings that are conspicuously marked with white in flight. Typically, the crest is not elevated in undisturbed *Lophotibis*, as illustrated in the accompanying photograph of a feeding individual (frontispiece). When alarmed the ibis raises its crest quickly and then lowers it.

Lophotibis is an exceedingly shy bird which feeds quietly on the forest floor during the day. While observed by Frank Gill in the forest at Ankarafantsika, an ibis appeared to pick up insects and millipedes from among the dry leaves on the ground. At dawn and dusk these ibises fly around uttering a loud, far-carrying, slightly raucous "work, work, work." The relationships of *Lophotibis* are uncertain, but we might speculate that it is closest to *Lampribus*, an African genus of shy forest-dwelling ibises which likewise have a bare face and a crest. Nevertheless, we do not regard *Lophotibis cristata* as really close to any living species, and we feel that it warrants a monotypic genus.

The Madagascar Crested Ibis has the dubious distinction of being the only Madagascar endemic currently protected by law in the Malagasy Republic. However, there are several rarer endemics there, as mentioned below. Furthermore, because of the great degree of endemism and other factors, concern is needed not just for the rarer species, but for the entire endemic Malagasy avifauna.

Madagascar has long been famous for the high levels of endemism in its avifauna. It boasts five endemic families (Mesitornithidae, Leptosomatidae, Brachypteraciidae, Philepittidae, and Vangidae, including *Hypositta*), one endemic subfamily (Couinae), and 39 endemic genera. Of the 187 breeding species (excluding seabirds and introduced species), no less than 129 (69 percent) are endemic at the species level, plus an additional 25 at the subspecies level. With the exception of one recent introduction, all but three resident passerine species are endemic.

The preservation of this magnificent avifauna should be a matter of the utmost concern. Man has probably already been directly responsible for several extinctions, including the flightless elephant-birds (Aepyornithidae). These birds were still present on the island when the first settlers arrived, about 1,000 years ago, and were doubtless exterminated by man and his animals. The cuckoo, *Coua delalandei*, largest of its kind and hunted both for food and its feathers, has not been reliably recorded since before 1834. A number of other species are extremely rare, e.g. *Eutriorchis astur* (Accipitridae), *Tyto soumagnei* (Tytonidae), and *Neodrepanis hypoxantha* (Philepittidae), although there is no evidence that man is directly responsible for the scarcity of any of them. Although the toll is disheartening, the avifauna is still relatively intact, and the Madagascar species list compares favorably with that of many other parts of the world. The situation is deceptive, however, and could change very rapidly for the worse—particularly through habitat destruction.

The endemic avifauna of the Malagasy Republic is dominated by species that are largely or wholly confined to various types of forest, i.e. 95 (74 percent) of the 129 species. The forests there, like those of so many other parts of the world, are being cleared and burnt at an accelerating rate to make way for agriculture. How much of the island was originally forested is unknown, but certainly it was much more than at present. According to aerial photographs, about 25 years ago there remained about 125,000 km² of forest, or 21 percent of the land surface (Chauvet, 1972. *The Forests of Madagascar*, in "Biogeography and Ecology in Madagascar," R. Battistini and G. Richard-Vindard (Eds.), The Hague, W. Junk. *Monographiae Biologicae* Vol. 21). Since that time more of the forest has been completely destroyed, at an estimated rate of 10–20 km² per year (Chauvet, *loc. cit.*). Our personal impression is that this estimate is far too conservative. On a flight up the east coast, which took us over the former range of *Coua delalandei*, we noted that Ile Ste. Marie was completely denuded of forest, as were most of the lowlands between Tamatave and Maroantsetra. Only scattered patches of scrubby second growth remained as evidence that the area was formerly forested. Observations from this and other flights lead us to think that only

about ten percent of Madagascar is forested today. Further, only 6,952 km² have been gazetted as nature reserves or national parks (1.2 percent of the land surface, 5.6 percent of the forest), and many of these reserves are not in key areas as far as birds are concerned.

There is little doubt that the endemic forest birds face extinction as their habitat is destroyed, starting with the rarest and most localized species. We know of only one locality each, for example, where the vangas *Xenopirostris polleni* and *X. damii* can be found. Add to this the fact that many forest birds seem ridiculously tame and sluggish, and some travel in flocks, thus making them vulnerable to indiscriminate collecting. Happily, the Malagasy Government is taking steps to control collecting that might threaten species of very local distribution.

In sum, the Crested Ibis and the many other endemic Madagascar birds are threatened with reduction of their numbers if not extinction. Of particular concern is the destruction of habitat, especially forest, but indiscriminate collecting is also a problem to be controlled.

We wish to thank Frank B. Gill for use of his photographs of the Madagascar Crested Ibis, which represent rarely obtained close-up views of this special species.

AMERICAN MUSEUM OF NATURAL HISTORY, CENTRAL PARK WEST, NEW YORK
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NEW LIFE MEMBER



Homer N. Metcalf is now a Life Member of The Wilson Ornithological Society. Mr. Metcalf holds degrees from the University of Connecticut (1939) and Cornell (1943), and he also attended Claremont Graduate School. He is a member of numerous biological and other societies and is a professor of horticulture at Montana State University. His principal interests in ornithology are centered on field observations. He lives in Bozeman, Montana, and is single.

STATUS OF THE PLAIN CHACHALACA IN SOUTH TEXAS

WAYNE R. MARION

The Plain Chachalaca (*Ortalis vetula mccalli*) is the only member of the family Cracidae in the United States, where it is native to four counties in the Lower Rio Grande Valley of Texas. The species' habitat of dense brushland and its shy, elusive nature make it difficult to observe in the wild. As a result, published information on the status of Texas chachalacas is meager. One report indicated that by 1940, severe reduction of suitable habitat, due to expanding agronomic production, and intense hunting pressure had reduced the population to 3,000 birds (Texas Game, Fish and Oyster Commission, 1945). Other reports (Blankinship, 1963; Evans, 1970; Hobson and Neikirk, 1970) have also referred to the loss of chachalaca habitat in Texas, but quantitative data have been scarce.

Suitable habitat for Plain Chachalacas in the Lower Rio Grande Valley includes isolated tracts of dense brushy woodland on relatively mesic sites. Vegetation in these areas consists predominantly of woody species, including granjeno (*Celtis pallida*), Texas sugarberry (*C. laevigata*), guayacan (*Portieria angustifolia*), and huisache (*Acacia farnesiana*). Other species often found in these woodlands include Texas ebony (*Pithecellobium flexicaule*), cedar elm (*Ulmus crassifolia*), honey mesquite (*Prosopis glandulosa*), and coma (*Bumelia lanuginosa*). Such habitats were rather widespread in earlier days in the Lower Rio Grande Valley (Clover, 1937) and were inhabited by chachalacas in southeastern Hidalgo County, nearly all of Cameron County, southeastern Willacy County, and a narrow strip along the Rio Grande in Hidalgo, Starr, and Zapata Counties to San Ygnacio (Texas Game, Fish and Oyster Commission, 1945; Aldrich and Duvall, 1955).

In view of the lack of detailed data on the species, I undertook this study, the objectives of which were: 1, to document recent reductions of suitable habitat within the natural range of chachalacas; 2, to determine the present distribution of chachalacas in Texas and compare this with the past distribution; and 3, to obtain a recent population estimate for chachalacas in Texas.

METHODS

The study of the status of Plain Chachalacas in the Lower Rio Grande Valley was conducted in extensive field work from January 1971 to August 1972. The main study area was Santa Ana National Wildlife Refuge, adjacent to the Rio Grande and southeast of McAllen, Texas. In addition, Cameron, Hidalgo, Starr, Willacy, and Zapata Counties were surveyed for determination of the distribution and abundance of chachalacas through extensive vehicular travel.

Distribution and abundance of chachalacas were determined during the 1972 breeding season by using a portable tape recorder and recorded calls to elicit calling responses from the species. Chachalacas call extensively during morning hours of the spring and early summer breeding season and respond readily during these times to recorded calls (at distances of up to 200 yards). The circular area within a radius of 200 yards of the tape recorder comprises 26 acres. This acreage was used in estimating bird densities, with census points established at 0.25 and 0.50 mile intervals adjacent to tracts of suitable habitat. Only those census points at which Plain Chachalacas actually responded to recorded calls were used in calculating density estimates. Each estimate was based on the ratio of calling birds to the acreage sampled.

Calculation of changes in suitable habitat was based on aerial photographs, with the extent of dense woodland, within the known natural range of this species in Texas, being measured with a planimeter. Aerial photographs from 1939 and 1971 were used for Cameron, Hidalgo, Willacy Counties, while for Starr County, where 1939 and 1971 photographs were not available, those from 1950 and 1968 were used.

The total chachalaca population in Texas was calculated using two correction factors; one for acreage known to contain chachalacas but not included in the survey and the other for noncalling birds in the population. All suitable chachalaca habitat could not be sampled during the survey, due to limitations on time and access to private properties. Acreage correction factors were calculated for each county using the ratio of known occupied habitat to the acreage sampled from census points.

Pairs of Plain Chachalacas generally call together during the spring, but my observations indicate that not all of these birds respond to recorded calls. In two instances the numbers of chachalacas inhabiting relatively distinct, isolated tracts were known. On one tract, 22 out of 50 (44 percent) chachalacas responded to recorded calls; on the other, 10 out of 17 (59 percent) responded. A correction factor for noncalling birds was calculated as the ratio of total number of chachalacas present to the number responding to recorded calls. In the two observations, approximately half of the chachalacas responded to recorded calls; therefore, an average correction factor of 2.0 was used to account for noncalling birds in the population.

Other data support the need for a correction factor when counts of calling chachalacas are used to estimate population size. Plain Chachalaca nesting transects indicated an adult breeding population density of approximately 1.2 birds per acre at Santa Ana National Wildlife Refuge. Approximately 0.5 Plain Chachalacas per acre responded to recorded calls at 10 census points on this area. From these data, a correction factor of at least 2.0 was necessary to adequately estimate chachalaca numbers from call counts at Santa Ana National Wildlife Refuge.

RESULTS AND DISCUSSION

The total acreage of suitable chachalaca habitat in the Lower Rio Grande Valley of Texas was severely reduced over the 32-year interval from 1939 to 1971 (Table 1). Highest reductions occurred in Hidalgo and Cameron Counties, where over 75 percent of the suitable chachalaca habitat present in 1939 was removed by 1971. Reduction in habitat occurred at a slower rate in Starr and Willacy Counties. This is particularly significant, as several hundred thousand acres of native brushlands were cleared in the Lower Rio Grande Valley prior to 1939 (Cottam and Trefethen, 1968).

TABLE 1
REDUCTION OF PLAIN CHACHALACA HABITAT IN THE LOWER RIO GRANDE VALLEY OF TEXAS,
1939 TO 1971.

| County | Chachalaca habitat present (acres) | | | | Percent reduction |
|--------------------|------------------------------------|--------|-------|--------|-------------------|
| | 1939 | 1950 | 1968 | 1971 | |
| Cameron | 40,113 | | | 9,841 | 75.5 |
| Hidalgo | 46,524 | | | 10,749 | 76.9 |
| Starr ¹ | | 10,822 | 6,513 | | 39.8 |
| Willacy | 3,356 | | | 1,629 | 51.5 |
| Total ² | 89,993 | | | 22,219 | 75.3 |

¹ Aerial photographs were not available for Starr County for 1939 and 1971; measurements were obtained from 1950 and 1968 aerial photographs.

² Excludes measurements from Starr County.

Major causes of habitat reduction were, and continue to be, expansion in residential development and agronomic production. Continued reduction of suitable habitat will lead to Plain Chachalacas being further restricted to sanctuaries and refuges in the Lower Rio Grande Valley of Texas.

Present distribution of Plain Chachalacas was found to be similar to that of an earlier survey by the Texas Game, Fish and Oyster Commission (1945), with one major difference: completion of Falcon Dam in 1953 inundated about 35 miles of chachalaca habitat along the Rio Grande in Zapata County and cut off the western tip of the natural range. The present distribution of this species in Texas thus extends from Falcon Dam southeastward along the Rio Grande in Starr and Hidalgo Counties to Weslaco, with an extension northeastward to Raymondville and the Gulf Coast in Willacy County (Fig. 1). This area includes the southern edge of Starr and Hidalgo Counties, southeastern Hidalgo County, nearly all of Cameron County, and southeastern Willacy County.

Within their range in Texas, Plain Chachalacas are generally restricted to isolated tracts of dense woodlands adjacent to irrigation reservoirs, canals, resacas (ponds), the Arroyo Colorado, and the Rio Grande. Approximately 71 percent of the remaining suitable habitat in the Lower Rio Grande Valley was in Cameron and Hidalgo Counties. Only about 23 percent and six percent, respectively, of the total remaining suitable habitat for Plain Chachalacas was in Starr and Willacy Counties (Table 2).

Percentages of habitat inhabited by chachalacas sampled during this study were 39.1, 20.7, 16.3, and 29.3 in Cameron, Hidalgo, Starr, and Willacy Counties, respectively. Acreage correction factors were based on these per-

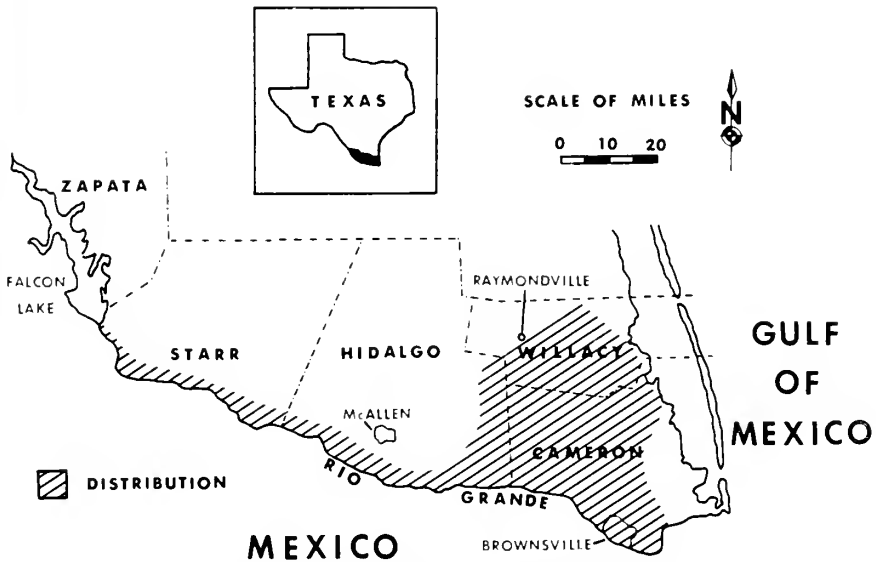


FIG. 1. Distribution of Plain Chachalacas in the Lower Rio Grande Valley of Texas, 1972.

centages and represent the ratio of occupied habitat to censused habitat (Table 2). These calculated values were 2.6, 4.3, 6.2, and 3.4 ($\bar{x} = 3.6$) for the respective counties.

Plain Chachalacas responded to recorded calls at 447 out of a total of 880 census points. At those points where birds responded, density estimates

TABLE 2
ESTIMATES OF SUITABLE HABITAT OF PLAIN CHACHALACAS IN FOUR COUNTIES OF THE LOWER RIO GRANDE VALLEY OF TEXAS, 1971-1972.

| | Dense woodland habitat in counties (acres) | | |
|---------|--|-----------------------|-----------------------|
| | Total extent ¹ | Occupied ² | Censused ³ |
| Cameron | 9,841 | 7,547 | 2,951 |
| Hidalgo | 10,749 | 9,287 | 1,919 |
| Starr | 6,513 | 1,839 | 299 |
| Willacy | 1,629 | 555 | 163 |
| Total | 28,732 | 19,228 | 5,332 |

¹ Determined from aerial photographs, all taken in 1971 except for Starr County, which was 1968.

² Measured from aerial photographs; chachalacas were known to inhabit these areas.

³ Estimated at each census point where chachalacas responded during the survey.

TABLE 3

ESTIMATES OF PLAIN CHACHALACA POPULATIONS IN THE LOWER RIO GRANDE VALLEY OF TEXAS, 1972.

| County | Chachalacas counted | Population ¹ size | Area sampled (acres) | Density (birds/acre) | Total ² population |
|---------|---------------------|------------------------------|----------------------|----------------------|-------------------------------|
| Cameron | 1,701 | 3,402 | 2,951 | 1.2 | 8,845 |
| Hidalgo | 971 | 1,942 | 1,919 | 1.0 | 9,322 |
| Starr | 71 | 142 | 299 | 0.5 | 880 |
| Willacy | 30 | 60 | 163 | 0.4 | 204 |
| Total | 2,773 | 5,546 | 5,332 | 1.0 | 19,251 |

¹ Obtained by multiplying the number counted by the correction factor for noncalling birds, i.e., 2.0.

² Obtained by multiplying the number counted by the correction factor for noncalling birds in the population and by an acreage correction factor (see methods).

(Table 3) for Cameron and Hidalgo Counties (1.2 and 1.0 birds per acre, respectively) were more than double those for Starr and Willacy Counties (0.5 and 0.4 birds per acre, respectively). The overall estimate of chachalaca densities in the four counties was 1.0 bird per acre. Plain Chachalacas were more abundant in Cameron and Hidalgo than in Starr and Willacy Counties (Table 3), as well as having a greater density. Overall, 2,773 chachalacas responding to recorded calls were counted in the four counties. After correction for noncalling birds and for chachalaca habitat not sampled, the Plain Chachalaca population was calculated to be 19,251 birds. My best estimate of the total chachalaca population in Texas is between 18,000 and 21,000 birds. An earlier estimate of only 3,000 chachalacas in Texas (Texas Game, Fish and Oyster Commission, 1945) is questionable, as it was apparently based on little quantitative data. The shy, elusive nature of this species has undoubtedly contributed to low estimates.

The overall trend in Plain Chachalaca numbers in Texas is unknown. However, a guess would be that there has been a slight increase in recent years despite the continued removal of suitable habitat (Table 1). Several factors may have contributed to this theoretical increase. Artificial feeding of chachalacas living in close proximity to people has undoubtedly increased their winter survival. Intensive land use has lowered predator numbers on some areas, resulting in diminished loss to this source of mortality. Also, Plain Chachalacas have been transplanted with some success within their natural range since 1959 (Blankinship, 1963; Evans, 1970; Hobson and Neikirk, 1970). Finally, this species has apparently adapted well to living in relatively small (1-5 acre) tracts of dense, woodland vegetation. This adaptability may facilitate further transplanting to additional, suitable, isolated tracts in Texas.

SUMMARY

The extent of habitat reduction, distribution, and population size of the Plain Chachalaca were studied in the Lower Rio Grande Valley of Texas. Suitable habitat, i.e., dense woodlands, has been severely reduced over much of the southern Texas range of this species. Expansion in agronomic production and residential development contributed largely to this reduction in habitat. The distribution of chachalacas in Texas includes much of Cameron County and portions of Hidalgo, Starr, and Willacy Counties. Density and abundance estimates were higher in Cameron and Hidalgo than in Starr and Willacy Counties. The overall density estimate for areas containing Plain Chachalacas in the Lower Rio Grande Valley was 1.0 bird per acre.

The total Plain Chachalaca population in Texas was estimated at between 18,000 and 21,000 birds. Trends in population size remain unknown, although artificial feeding by local residents, reduced predatory pressures, and initiation of transplanting programs may be responsible for slight increases in Plain Chachalacas in recent years. Additional transplanting of birds to suitable, unoccupied areas within their natural range may benefit chachalaca populations in Texas.

ACKNOWLEDGMENTS

I acknowledge with thanks financial assistance from the Caesar Kleberg Research Program in Wildlife Ecology at Texas A&M University. Sincere thanks go to W. H. Kiel, Jr. for his advice and encouragement during this study. I am also indebted to Drs. K. A. Arnold, S. L. Beasom, J. D. Dodd, T. M. Ferguson, and J. G. Teer for their critical review of the manuscript. Aerial photographs were generously provided by several federal agencies in the Lower Rio Grande Valley, including the International Boundary and Water Commission, the Soil Conservation Service, and the Agricultural Research Service of the USDA. This paper is part of a dissertation in partial fulfillment of requirements for the Ph.D. degree at Texas A&M University. This is Texas Agricultural Experiment Station Technical Article No. 10973.

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STUDY OF BREEDING RAILS WITH RECORDED CALLS IN NORTH-CENTRAL COLORADO

JAMES F. GLAHN

The Sora (*Porzana carolina*) and Virginia Rail (*Rallus limicola*) are two of the most widespread species of rails in North America. Because of their secretive habits and dense habitats, estimating and studying their breeding populations has been a difficult task. The two most intensive field studies of Sora and Virginia Rail populations used nest surveys to estimate breeding populations (Pospichal and Marshall, 1954; Tanner and Hendrickson, 1954, 1956). These estimates are biased by the fact that rail nests are usually so well-concealed that some would be missed even after an intensive search. Direct counts or flushing counts, as used by Boeker (1954), have obvious disadvantages in species that are seldom seen and rarely flushed. In an attempt to improve censusing and study of rail populations, I used tape-recorded calls in marshes in north-central Colorado. My aims were two: to determine the distribution of nesting territories and breeding densities of Sora and Virginia Rails; and two, to evaluate elicited call counts as a census method and relative index for rail populations.

The calls of rails are probably the best indication of their presence in an area. In Alberta, Smith (1955) counted Soras by their *keek* (distress call) note, eliciting this by throwing rocks into potholes. Meanley (1957) studied the distribution of the King Rail (*R. elegans*) territories by the positions of their mating calls. Post and Enders (1970) spot-mapped the calls (and nests) of Virginia Rails to determine breeding densities of a saltmarsh population. Adams and Quay (1958) investigated using call counts of the Clapper Rail (*R. longirostris*), although they concluded that the calls were too variable in time and number to be useful as a census method. More recently, Tomlinson and Todd (1973) used recorded calls to study distribution in two western races of Clapper Rail and felt that the recorded call technique could be used to develop a population index for this species.

METHODS AND MATERIALS

Sora and Virginia Rails use two principal calls during the breeding season that seem to fit Meanley's (1969) functional scheme of classifying rail calls. The mating call of each species is probably used exclusively by the male to attract a mate (Bent, 1926). The primary advertising calls are given by both sexes throughout the breeding season and function as a territorial call and as a contact call between mated pairs (Kaufmann, 1971). The primary advertising call of the Sora is usually described as a "whinny," varying in number of notes and descending in frequency and amplitude. The primary

advertising call of the Virginia Rail is usually described as a "grunt," resembling the grunt of a domestic pig, which descends in frequency towards the end of the call.

Tapes were made of both types of calls from two Cornell University Records: American Bird Song Vol. 2 and Field Guide to Western Bird Songs. A Uher Model 4000 tape recorder was used to transcribe these calls and to broadcast them in the field. Amplitude measurements were made by playing back these recordings at full volume with the tape recorder 1 m from a sound level meter in the laboratory. The audible sound pressure produced ranged from 93 to 96 db. Several of these calls recorded locally in the field were compared by sonograph analysis to those taped from records. There was some slight detectable variation, but no important change in the overall temporal or frequency patterns.

Preliminary trials with these tapes on four small marshes in the Fort Collins area, during spring 1968, indicated that taped calls consistently elicited more responses from rails than did disturbances, such as throwing rocks in the water. Rails would respond either singly or in duets of mated pairs. Kaufmann (1971) indicates that the male starts the call and may be joined by the female before he had finished his call. It definitely appears that this type of duet response could be used to locate positions of breeding pairs. Trials on ten Virginia Rails and six Soras during April and May 1968 indicated that both species would respond repeatedly to their primary advertising calls during the breeding season. I concluded from these preliminary investigations that it would be feasible to census these rails by conducting several response surveys during the breeding season.

Three marsh areas, surrounding Fossil Creek Reservoir, approximately eight miles southeast of Fort Collins, Larimer County, Colorado, were selected for intensive study during spring 1972. All three areas comprised approximately 10 hectares of type 3 and type 4 wetlands (Martin et al., 1953). A network of narrow channels flows from Fossil Creek and from other tributaries of the reservoir. Cattails (*Typha latifolia* and *T. angustifolia*) comprised approximately 90 percent of the emergent vegetation on all three study areas. Bulrushes (*Scirpus paludosus* and *S. fluviatilis*), threesquare (*Scirpus americanus*), spikerush (*Eleocharis obtusa*), and saltgrass (*Distichlis* sp.) dominated the drier peripheral zone around the cattail. Water depths in the emergent zone ranged from zero to approximately 80 cm, with fluctuations of 12 to 15 cm during the breeding season (April to June).

In late March, all three areas were surveyed and a grid system set up, with flagging tape attached to dead vegetation at 30 m intervals. Gridded maps with a 1:1200 scale were made from surveying measurements. A fresh photocopy of these maps was used during each survey of the area to spot-map "vocal registrations" of responding rails. A standard route for each area was selected by following transect lines 60 m apart in a zig-zag pattern, with alternate starting points used during each successive survey. A 5-minute tape, consisting of 10 calls of each species, was played at stations 60 m apart along each of the routes. Approximately one-half of the total study areas was surveyed during the first three hours after sunrise and the other half during the last three hours before sunset of the same day. Morning and evening surveys were alternated between areas. Surveys were conducted only when wind velocities were less than 15 mph, under varying degrees of cloud cover. Ten semiweekly surveys were made from 26 April to 28 May, with an interval of at least two days between surveys. Terminology and procedures for evaluating census data followed the international standard for the mapping method in bird census work (Svensson, 1970).

As soon as rail territories were located, tests were made on single and paired rails to measure individual response to tape recordings. These tests were made with different

tapes from those used during censusing, some of which were recorded locally. Data were collected on the calling frequency in equal 5-minute periods—before, during, and after the playback of the taped calls. The estimated initial distance at which individuals responded and the number of taped calls to elicit the first response were also recorded. After most of the censusing had been completed and the distribution of territories was better known, trials were made from stations near the center of several territories to determine the percentage of territories responding to the taped calls during several 5-minute trials.

Nest surveys were made from approximately mid-May to mid-July. Systematic searches proved unrewarding, and later most nests were discovered by intensely searching areas where both rails were heard giving *keep*-like calls. Most nests were found while young were leaving them, although the adults were still on territory.

RESULTS AND DISCUSSION

Territory Formation and Breeding Densities.—In two field seasons, no responses were elicited from rails prior to mid-April, although initial surveys were started by 1 April. Earliest responses coincided with the first shoots of cattail emerging above the water. Both species are reported to arrive in this area in early April, but they may be silent for sometime after arrival (Niedrach and Rockwell, 1939).

The initial formation of territories was indicated by the mating calls of the males. *Tick-it* calling of the Virginia Rail was heard primarily from 13 April to 28 April, while the *ker-wee* call of the Sora was heard primarily from 13 April to 5 May. These periods seem to coincide with the arrival and brief courtship period of these two species. Mating calls elicited later in the breeding season could be attributed to unmated males, which formed "surplus registrations" from spot-mapping.

During the census period, 371 registrations were made, including 12 percent visual and 88 percent vocal. Based on maps of calling birds and 14 nest sites found, an estimated 18 pairs of Virginia Rails and six pairs of Soras were breeding on the 10-hectare study area. In 1968, with no distinction made between paired and unpaired rails, 10 Virginia Rails and six Soras were located with recorded calls. Annual spring counts and literature concerning this area do not reflect this almost three to one ratio in relative abundance of these species indicated from this study, although Neilson (1925) noted that Virginia Rails were about twice as common as Soras near Wheatland, Wyoming.

Distribution of Nesting Territories.—Spot-mapping (Figs. 1–2) indicated that, on the study areas, all six Sora territories apparently overlapped to some extent at least one Virginia Rail territory. Often these two species were spot-mapped concurrently less than 10 m from one another. In other observations,

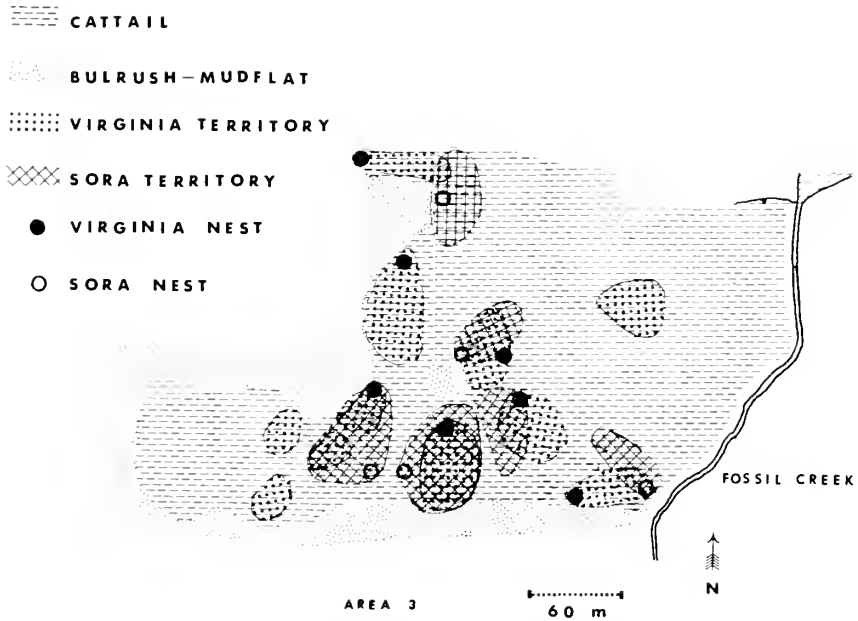


FIG. 1. Distribution and habitat association of Sora and Virginia Rail territories on area 3.

Sora and Virginia Rails were seen using the same feeding areas, and on one occasion, were observed feeding side by side.

All of the nest sites found were within the territories defined by spot-mapping responses. The least distance between occupied Sora nests was 12 m, between Sora and Virginia nests 25 m, and between two Virginia nests 23 m. This may indicate more intraspecific tolerance between Soras than Virginia Rails. Others (Pospichal and Marshall, 1954; Tanner and Hendrickson, 1954) have reported larger nesting distances between Virginia Rails than Soras, but attributed it to the lower breeding densities of Virginia Rails.

The relative position of nest sites in habitat types appeared to be an important aspect of the requirements of breeding rails (Figs. 1-2). Although cattail formed the dominant cover in all territories, 83 per cent of Virginia territories and all of the Sora territories were bordered by bulrush, spikerush, saltgrass, and by mudflats. Both rail species were often observed feeding in these edges, but they sought dense cattail cover when disturbed. Although all nests were constructed of cattails and located or supported in these plants, 77 percent of the Virginia nests and all of the Sora nests were within 15 m of edge vegetation bordering each territory. Allen (1934) stated that both rails

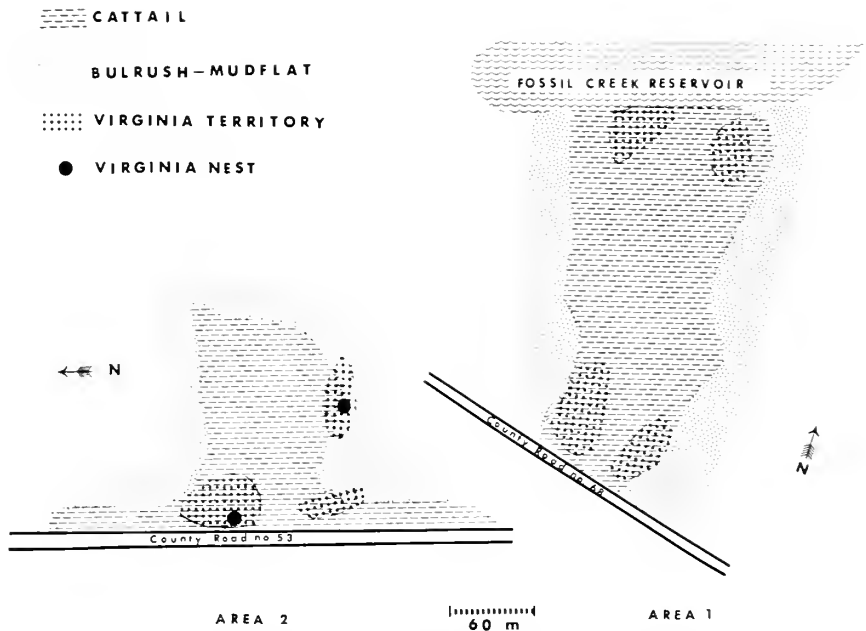


FIG. 2. Distribution and habitat association of Virginia Rail territories on areas 1 and 2.

prefer nesting near the borderline between sedges and cattails. Later Pospichal and Marshall (1954) found a similar relationship between nest location and edge of heavy cover.

Index Value of Response Behavior.—From 13 April to 25 June, approximately 50 hours of observation were spent in studying responses to tape recordings of Sora and Virginia Rails. Playback of taped calls significantly increased the rate and frequency of calling. During 50 trials of five minutes per period, the playback of taped recordings increased the frequency of calls from 31 prior to playback to 134 during the playback period. The non-elicited calling rate during these trials was less than six calls per hour of observation, while the elicited calling rate was greater than 25 calls per hour of observation.

At an amplitude between 93 and 96 db at 1 m, responses were obtained from both rails up to approximately 80 m, but 90 percent of the responding rails were located within 60 m of the speaker. Within this radius, the number of individuals responding varied from trial to trial, but all individuals appeared to respond after a total of three consecutive 5-minute trials. Responding individuals called at a rate of one to three times during a 5-minute

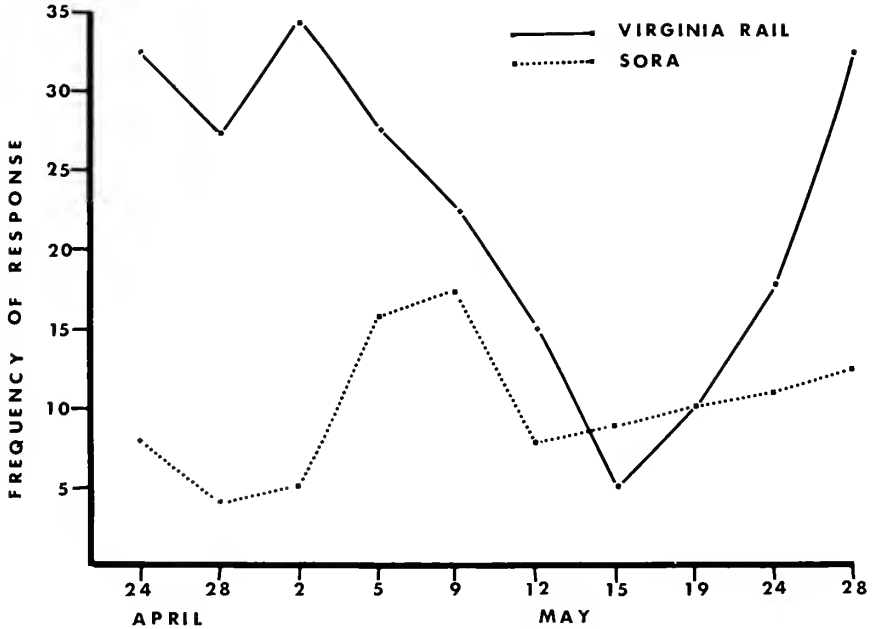


FIG. 3. Frequency of response to taped calls during 10 semiweekly surveys.

playback. At low density levels, individuals only responded once during a 5-minute trial. A previous response or non-elicited call by an individual reduced the chance of that individual responding again during the same trial. The number of taped calls needed to elicit the first response ranged from one to a total of 10 calls on the tape, although 79 percent responded during the first five calls and 35 percent responded after the first call. Sora and Virginia Rails responded as readily to each other's calls as they did to their conspecific calls, with no apparent difference between the number of recorded calls to elicit intra- and interspecific responses. Duet recordings of breeding pairs for both species appeared to be more effective than tapes of single birds in eliciting responses from rails during the nesting period. During this period, rails responded to duet tapes immediately after failing to respond to a single rail tape.

Fluctuations in the frequency of response were found during 10 semi-weekly surveys of the study areas (Fig. 3). Although all breeding pairs were estimated to be on territory by 5 May, the calling frequency of Virginia Rails fluctuated considerably after this time, while the frequency of Sora calling began to stabilize a week later. Kaufmann (1971) indicated that normal calling activity of both species fluctuated during the breeding cycle, forming two

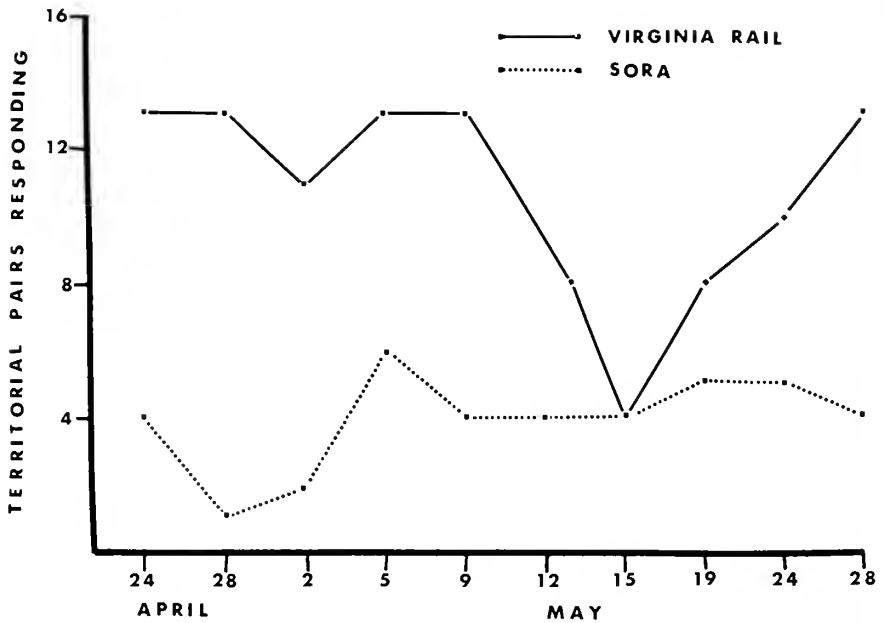


FIG. 4. Number of territorial pairs responding to taped calls during 10 semiweekly surveys.

peaks coinciding with the start of egg laying and with hatching. These fluctuations appeared to be primarily a function of the percentage of territorial pairs responding during each survey (Fig. 4). During all 10 surveys the frequency of territorial pairs responding was estimated to range from 20 to 100 percent for Soras and from 22 to 72 percent for Virginia Rails. From 5 May to 28 May, the estimated percentage of territorial Virginias responding ranged from 22 to 72, while the percentage of Soras responding varied only from 67 to 100. Although both species of rails responded to taped calls as late as mid-August, only a small percent of those observed to be present responded after the last part of June.

Higher breeding densities appeared to increase the frequency of responses from Virginia Rails. Kaufmann (1971) noted that Sora calling increased greatly with an increase of breeding pairs on one study area over several years of observation. Table 1 summarizes responses obtained from Virginia Rails during the census of three separate study areas, and similar data are presented on Sora Rails which bred on only one of the study areas. As these data indicated, both the mean calls per hectare and mean calls per territory increased with the breeding densities of Virginia Rails on each study area. The disproportionately high frequency of Sora calling on area 3 may have

TABLE 1
RESPONSE CALLING AND BREEDING DENSITIES OF RAILS FROM 10 SURVEYS OF THREE STUDY
AREAS IN COLORADO

| Species and area | Calls per hectare (\bar{x}) | Territories per hectare | Calls per territory |
|------------------|---------------------------------|-------------------------|---------------------|
| Virginia Rail | | | |
| Area 1 (2.9 ha) | 1.5 | 1.4 | 1.1 |
| Area 2 (1.3 ha) | 3.0 | 2.3 | 1.3 |
| Area 3 (5.8 ha) | 2.4 | 1.9 | 1.3 |
| Sora | | | |
| Area 3 (2.9 ha) | 1.6 | 1.0 | 1.6 |

been influenced by the large number of Virginia Rails on this same area. Dow (1970) indicated that responses of certain individuals to recordings may increase the stimulus value of recordings for other conspecifics within hearing range. This was apparently true of Virginia Rail responses and is further confounded by the fact that rails respond interspecifically to each other's calls.

Although individual response counts would appear too variable in time and number to be used as an index in themselves, recorded calls did increase rail calling to a predictable level where censusing by spot-mapping response was practical. Censusing with recorded calls provided a good estimate of population densities, and in comparison with nest surveys, increased the number of territories located by 71 percent. This technique appears to provide a more accurate appraisal of the relative abundance of each species with respect to more conspicuous species, and it could be used in obtaining annual indices of Sora and Virginia Rail populations.

SUMMARY

A method of estimating Sora and Virginia Rail populations by spot-mapping responses to tape recordings of their primary advertising calls was devised and tested in north-central Colorado. Individual response counts appear to be affected by stages of the breeding cycle and relative breeding densities on each area. Within the response radius of 60 m, a 5-minute playback period, preceded by five minutes of no calling, appeared to be adequate in eliciting responses from a large percentage of rails without counting a single individual more than once. The recorded-call technique provided a satisfactory means of censusing and studying territory distribution of breeding rails.

ACKNOWLEDGMENTS

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NOTES ON THE LIFE HISTORY OF THE YELLOW-BREASTED FLYCATCHER IN SURINAM

F. HAVERSCHMIDT

The Yellow-breasted Flycatcher (*Tolmomyias flaviventris*) is one of the many medium-sized greenish flycatchers of tropical South America. The genus *Tolmomyias* comprises a group of four rather large-headed, flat-billed birds. Besides the above, these are the Yellow-olive Flycatcher (*T. sulphurescens*)—the largest; the Yellow-margined Flycatcher (*T. assimilis*); and the Gray-crowned Flycatcher (*T. poliocephalus*)—the smallest. In the field in Surinam, *T. flaviventris* is easily distinguished from the others in having the crown olive-green, concolor with the back and wings, whereas the crown is grayish in the local *T. sulphurescens* and *T. assimilis* and slate-gray in *T. poliocephalus*. *T. flaviventris* has the entire underparts yellow, more ochraceous on the throat and breast. Its length is about 5 inches; the weights of specimens collected by me in Surinam are: 11 ♂♂, 13 g (12–14); 13 ♀♀, 13.4 g (12.5–15.5).

In Surinam, *T. flaviventris* is quite common in the mangroves (*Avicennia nitida*), wherever they form a continuous forest of tall trees. It is equally common in the shade trees (*Erythrina*) of coffee plantations, a vanishing habitat in Surinam, now that such plantations are gradually being broken up. In the mangroves it is the only representative of *Tolmomyias*, but in the coffee plantations *T. poliocephalus* also occurs, albeit rarely. I have never found *T. flaviventris* outside the coastal plain in the savanna region. It also seems absent in the forests to the south, where *T. poliocephalus* and *T. sulphurescens* are found, the latter also quite commonly at forest edges. Outside the breeding season *T. flaviventris* is an unobtrusive, solitary, and arboreal bird, making itself conspicuous only by a high pitched and shrill “tchee-ee.” It feeds at a moderate height, taking insects in flight from among the foliage: only very seldom does it dart after flying insects.

Skutch (1960) published an extensive life history of *T. sulphurescens* in Central America, and I have given a summary of the nesting habits of *T. flaviventris* in Surinam (Haverschmidt, 1968). In the present article I will give the details, together with some additional observations. The breeding habits of *T. flaviventris* seem almost identical with those of *T. sulphurescens*, as described by Skutch.

DISPLAY

Skutch (loc. cit.) mentions no displays in *T. sulphurescens*, and I have observed what I consider to be displays of *T. flaviventris* only three times. On 10 May 1962, I watched two birds in my garden moving about in the trees.

One of them, while uttering a chirruping sound, made waving movements with one wing, closing it after each wave. The second bird came near but nothing further happened. Again the next day two birds were seen among the same trees. One of them made waving movements with its wings, alternating between the left and the right wing, but always with only one wing waving at the time: the closed wing was held somewhat loosely. I expected copulation to occur in this instance, but it did not follow. On 21 June 1962 in my garden, a nest was under construction—this consisting of only a few fibers hanging over a branch. A bird arrived with nest material in its bill, while another sat nearby. The sitting bird suddenly started slow, waving movements with its wings, alternating the left and the right wing, one at a time. The crown feathers were erected, forming a minute crest. Once more nothing happened in response, and the nest building did not continue; the fibers were later blown away and I did not see the bird anymore. Skutch (1960:364) reports a similar wing-waving behavior in *Pipromorpha oleaginea*, but I have not seen it in Surinam.

THE NEST AND NEST-BUILDING

The nest of *T. flaviventris* is a pensile, retort-shaped purse with an orifice on the bottom at the side (Fig. 1). The nest is attached to slender, usually leafy twigs, and is made of what Skutch (op. cit.) aptly calls "vegetable horse hair," i.e. fine fibrous roots taken from branches. All the nests I have seen had a yellowish color, in contrast to those of *T. sulphurescens*, which were brownish black or black. Most of the nests are quite conspicuous and easy to locate, but are high up in trees and out of reach. I was able to inspect only seven nests, these at heights of 1½ to 3½ meters. In Surinam most nests of *T. flaviventris* are in close proximity to inhabited wasp nests. Out of 54 nests seen, including deserted ones, 41 (76%) were near a wasp nest, either of the large *Synoecca surinama* (which makes long corrugated nests plastered against the main stem of trees or strong branches) or of the smaller *Polybia* species (which make small saucer- or box-shaped nests attached to slender twigs). Wasp nests apparently have an attraction for several species of birds. On 4 June 1950, a Yellow-breasted Flycatcher and a female White-winged Becard (*Pachyramphus polychopterus*)—a species which very frequently nests near wasp nests in Surinam—tried to build at the same spot near a wasp nest. The becard, although considerably larger (weight about 21 gm), never succeeded in getting a foothold, as it was constantly driven away by both the flycatchers.

As previously reported (Haverschmidt, 1954), on 27 September 1953 I found a nest of the Southern Beardless Tyrannulet (*Camptostoma obsoletum*) fastened to an old *Tolmomyias* nest, near a wasp nest. On 6 July 1958, there



FIG. 1. Nest of *Tolmomyias flaviventris* in Surinam.

was a nest of a Yellow-breasted Flycatcher amidst a colony of Yellow-rumped Caciques (*Cacicus cela*), again near a large wasp nest. Old nests of this flycatcher are sometimes pilfered and the nest material used for building their new nests. On 29 January 1951, a nest was made on the remnants of an old one that I had found occupied on 23 July 1950—also near a wasp nest.

Nest-building is by the presumed female only, but what must be the male often accompanies the building bird, although I never saw him carrying material. Building may be carried on at a rapid rate. On 29 July 1952 a bird arrived with nest material 23 times during one hour of observation. The nest was in a deteriorated state on 8 August, and a new one was started immediately below it, once more near a wasp nest. On 22 April 1960 I found the beginning of a nest—consisting of a few fibers—hanging on a branch of a *Lagerstroemia* tree in my garden. The nest was at a height of about 3½ meters, near a small wasp nest identified as *Polybia occidentalis*. Although the bird was constantly at work, progress was slow, and the retort shape was first apparent on 2 May. On 22 May it looked completed, but by carefully inserting one of my fingers I could establish that there were still no eggs. On

26 May it contained one egg: nest-building therefore had lasted 34 days. On 27 May at 17:00 there was still one egg and on 28 May at 17:00 there were two eggs, completing the clutch. As in *T. sulphurescens* (Skutch, 1960), the eggs had been laid on alternate days. The eggs are creamy white with a few scattered dark purplish spots, mostly at the large end.

A clutch consists of 2 or 3 eggs. Of the 7 nests I was able to inspect, one had three eggs (3 May), two had three nestlings (22 June and 3 August), three had two eggs (28 May, 18 and 20 July), and one had a single nestling (9 June). The breeding season is a protracted one, with 38 occupied nests found as follows: January (2), April (1), May (8), June (10), July (10), and August (7). Two nests under construction were also found in September. These data show a predilection for the long rainy season, which lasts from mid-April until mid-August.

INCUBATION

Only one bird, presumably the female, incubates; I never saw the second bird take part. The first egg of the nest in my garden (clutch of 2 eggs completed on 28 May) hatched on 13 June at 15:30 and the second egg on 14 June at 7:00. The incubation period was thus 17 days. The eggs hatched on successive days, agreeing with what Skutch (1960) established for *T. sulphurescens*.

THE NESTLING PERIOD

The nestlings hatch naked, devoid of any down. They are dark in color; the inside of the mouth is yellow. They were fed by both parents, the food consisting of small insects—delivered to them one at a time. Prey was taken in flight from among the foliage, sometimes immediately below the nest. The bird bringing food alighted at first on a branch nearby; from there it shot right into the entrance to the nest, never clinging to the nest wall. When one bird was inside, either feeding or brooding the nestlings, the other one repeatedly tried to enter. The latter never succeeded, having to wait until the other bird left the nest. Excrement was taken away rather than eaten. The nestlings were no longer brooded after the age of 5 days. A summary of the feeding rate and the covering of the nestlings is given in Table 1.

On 23 June, when the nestlings were 9 days old, they were very noisy, peeping constantly and clearly audible when I stood at the nest tree. This made the nest quite conspicuous. As I did not see the birds on 27 June, I inspected the nest and found that it contained a single dead nestling; the other had disappeared. The nest was wholly intact, not damaged or out of shape, so I believe that it had been robbed previously by a snake. At any rate, the nestling period could not be established.

TABLE 1
SUMMARY OF THE CARE OF NESTLINGS

| Date observed | Age of nestling | Time observed | Times fed | Time nestlings brooded | |
|---------------|-----------------|---------------|-----------|------------------------|---------|
| | | | | periods | minutes |
| 16 June | 2 days | 16:55-17:55 | 12 | 17:08-17:15 | 7 |
| | | | | 17:47-17:52 | 5 |
| 17 June | 3 days | 15:50-16:50 | 16 | 15:50-15:55 | 5 |
| | | | | 16:02-16:04 | 2 |
| | | | | 16:06-16:19 | 13 |
| | | | | 16:24-16:33 | 9 |
| 18 June | 4 days | 10:40-11:40 | 14 | 10:51-10:56 | 5 |
| | | | | 11:03-11:08 | 5 |
| | | | | 11:10-11:19 | 9 |
| | | | | 11:30-11:38 | 8 |
| 19 June | 5 days | 14:15-16:15 | 18 | none | none |
| 23 June | 9 days | 15:30-16:30 | 24 | none | none |

ENEMIES AND SECONDARY TENANTS OF NESTS

Apart from being robbed, apparently by snakes, occupied nests are sometimes pilfered by other birds. On 31 July 1949 a Gray-crowned Flycatcher (*T. poliocephalus*) repeatedly took nest material from an occupied nest of a Yellow-breasted Flycatcher. This it used for its own nest, under construction near a small wasp nest (Haverschmidt 1950). The *T. flaviventris* nest became so badly damaged that it was deserted.

Occupied nests were also taken over by Piratic Flycatchers (*Legatus leucophaeus*). On 17 March 1957 and on 3 October 1952 I observed pairs of the latter species feeding nestlings in nests of the Yellow-breasted Flycatcher. They fed their nestlings as they clung to the entrance.

SUMMARY

In Surinam, the Yellow-breasted Flycatcher inhabits tall mangroves and shade trees in the coffee plantations in the coastal plain. It feeds on small insects plucked in flight from among the foliage. The call is a shrill and high pitched "tchee-ee." A display consisting of slow waving movements of the wings moved alternately, was observed. The nest is a pensile, retort-shaped structure with the entrance at the bottom on the side, attached to slender twigs and usually at a great height. The presumed female alone builds the nest of yellowish fibers; building lasted 34 days in one case. Most nests (76 percent) are built near wasp nests. The 2 or 3 eggs are laid on alternate days and only the female incubates. Incubation lasted in one case 17 days, the eggs hatching on successive days. The nestlings are dark in color at hatching and devoid of down. They are fed on insects—one at the time—by both parents. They are brooded by one of the parents until the 4th day. The breeding season is a protracted one but mainly during the long rainy season. Apart from being robbed by snakes, the nests are sometimes pilfered by other birds and taken over by the Piratic Flycatcher.

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16 WOLFSKUILSTRAAT, OMMEN, HOLLAND. ACCEPTED 26 NOVEMBER 1973.

NORTH AMERICAN NEST RECORD CARD PROGRAM

Cornell Laboratory of Ornithology is promoting two special projects in its North American Nest Record Card Program for 1974, in addition to regular collection of nesting data. With the support of the World Wildlife Fund, the Laboratory has set up a national register of birds-of-prey to monitor their breeding success in the wild. This register is an independent section of the existing Nest Record Card Program, but information will be collected on regular nest record cards. Details of nest locality will be kept secret and maintained in a master file, from which data will be released only with permission of both the original investigator and the Laboratory. Data will go back many years, so breeding success can be calculated over a long period and annual variations and long-term alterations can be seen. These data will pinpoint species and areas of concern that will enable action to be taken.

The second special research area deals with colonial nesting, such as in certain wading birds.

The Laboratory makes a special appeal for nesting records of raptors and colonial nesting birds; however, nesting data on *all* species of birds of North America will continue to be collected. This includes data from previous years, and researchers with large amounts of original data are invited to inquire about ways of putting these data into a form that will be of permanent value to science.

VOCALIZATIONS OF THE MOUNTAIN PLOVER

WALTER D. GRAUL

The Mountain Plover (*Charadrius [Eupoda] montanus*) is a little-studied endemic species of western North America, breeding on the shortgrass plains mainly east of the Rocky Mountains and wintering from California and Texas to northern Mexico. Apart from a few anecdotal reports, information on the breeding biology of the species has come from a single study (Laun, 1957). In 1969, I began a study of the Mountain Plover on its breeding grounds in Colorado. The present paper describes the vocalizations of the species, which to date have been among the most meagerly reported (e.g. Bent, 1929) of any North American plover. Other aspects of the behavior of this species have been published elsewhere (Graul, 1973a, 1973b) or are in preparation.

Formerly, this species was placed in such genera as *Podascys* or *Eupoda*, but recent workers such as Bock (1958) and Jehl (1968) consider the species to be in the genus *Charadrius*, an opinion with which the A.O.U. (Eisenmann et al., 1973) now agrees.

STUDY AREA AND METHODS

I studied these plovers on two study areas in northern Weld County, northeastern Colorado. The major areas consisted of 16 km² just southwest of Keota. The secondary area was on the International Biological Program's Pawnee Site, approximately 64 km northwest of Keota. I spent the following periods on the study areas: 18 March–15 August 1969; 25 May–29 May 1970; 1 June–31 July 1971; 31 March–19 May 1972.

Vocalizations were recorded with a Uher 4000 Report-L tape recorder and Uher A-13 microphone (with parabola for two calls) at a tape speed of 7½ inches per second. Audiospectrograms were prepared with a Kay Electric Company Sonograph using a wide band-pass filter.

RESULTS

To the human ear the vocal repertoire of the adult Mountain Plover seems to consist of several distinct calls. During my work on this species, I obtained limited recordings of most of these calls. These vocalizations are described mainly qualitatively, and additional research is needed to quantitatively describe any variability in them.

Wee-wee Call.—This call (Fig. 1A) consists of a single note repeated rapidly in series. It is given by both sexes on the ground and in an aerial display (Graul, 1973b). The call is also frequently uttered by birds during aggressive encounters. Although commonly given during the prenesting and early nesting periods, the call is rarely heard once nesting is in full progress. On one occasion, a male attending a brood suddenly stopped injury-feigning and gave this call. Sometimes several members of a fall flock utter the call si-

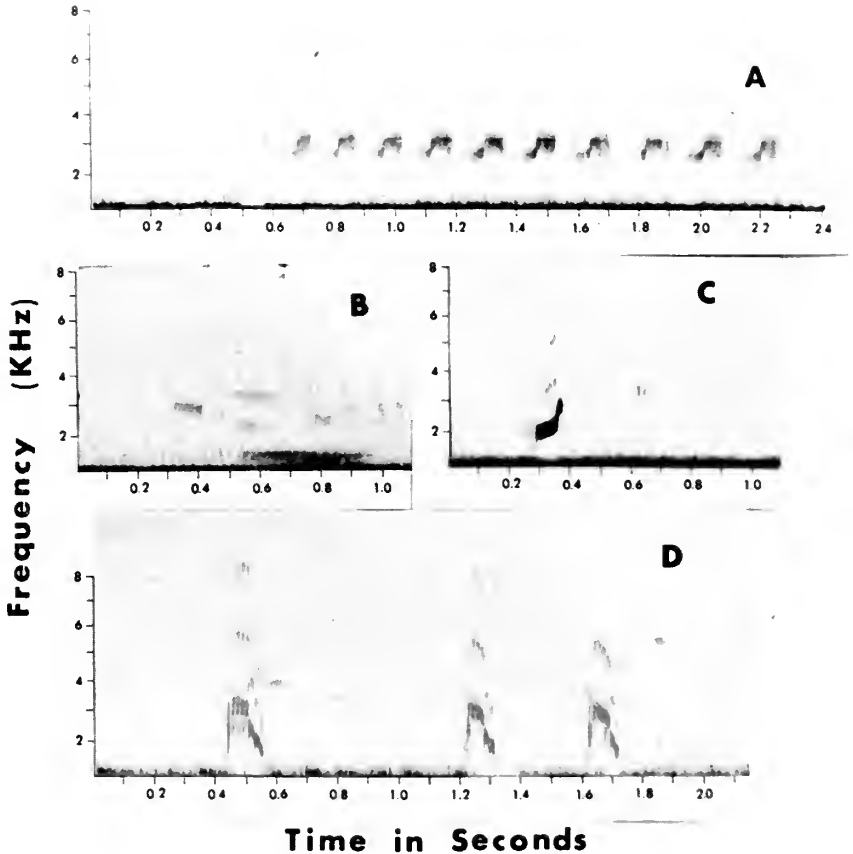


FIG. 1. Audiospectrograms of Mountain Plover calls: A, Wee-wee; B, Mooing (low vocalization at 0.5-0.9 sec.); C, Tu-lup (at 0.3 sec.); D, Ke-op.

multaneously. The calls recorded by me have a frequency between 2.5 to 3.5 KHz. with a fundamental frequency of about 3.0 KHz. The calls are about 0.1 sec in duration, with the interval between calls about the same. I detected no harmonics on my audiospectrograms.

Mooing Call.—This call is given during Bowing, a major courtship display (Graul, 1973b). It is a low, soft sound (Fig. 1B), strikingly similar to a cow mooing in the distance. The display and call are usually given by males, but I did record one female giving them in response to Bowing by a male. The calls have a frequency between 0.0 to 1.0 KHz. and I detected no harmonics on my audiospectrograms. The calls are about 0.1 sec in duration, with the interval between calls about the same.

Chert Call.—This call consists of a short, soft note repeated in series; it is given by a male, in the Upright Precopulatory Posture (Graul, 1973b), as he approaches a female prior to mounting. I was unable to record the call, as males terminated calling as I approached them.

Tu-lup Call.—Frequently, an adult attending a nest or its brood initially responded with this call (Fig. 1C). It was typically given by a bird as it stood in an alert posture, repeatedly flicking its head back while keeping its bill parallel to the ground. This is an anxiety movement typical of many species of Charadrii (Maclean, 1967). The calls recorded by me have a frequency between 1.0 to 3.5 KHz and consist of a two-part unit, with the second part at a higher frequency than the first. The calls are about 0.1 sec in duration, but I lack data on the interval between calls. There are two very weakly developed harmonic bands.

Ke-op Call.—This call was given in the same context as the preceding call. On some occasions one or the other was given alone, but frequently the two calls were mixed in a single series. This call (Fig. 1D), as in the Tu-lup Call, is a two-part unit, but the frequency drops in the second part and has a range of about 1.0 to 3.5 KHz. The calls are about 0.1 sec in duration, with the interval between them varying between about 0.3 to 0.7 sec. Weakly developed harmonic elements are present.

Kip Call.—This is a short note produced in rapid series, but I was unable to record it. Occasionally, when I released a captured bird it would fly away giving this call. Frequently, when one bird chased another in the air the call was given, but I could not ascertain which bird did the calling.

Clicking Call.—Three adults responded with this call as an observer crouched beside their respective nests. The call is a barely audible, mechanical sounding note (Fig. 2A): it is produced in irregular bursts as the bird moves slowly, in the Tail-down Rush Posture (Graul, 1973b), towards the intruder. A given note sounds like a single unit to the human ear, but it appears from my audiospectrograms that each note is actually composed of two parts. The first part has a frequency between about 1.0 to 4.5 KHz and the second part has a frequency range between about 2.0 to 3.0 KHz. Each note has a duration of about 0.02 sec and the interval between notes within a single burst ranges from about 0.02 to 0.03 sec. I detected no harmonics on my audiospectrograms.

Chatter Call.—This call was given immediately following the preceding call by the above three birds. It was uttered as a bird suddenly moved quickly toward the intruder; it is a series of loud, harsh notes (Fig. 2B). The calls recorded by me have a frequency between 3.0 to 4.0 KHz. They range from

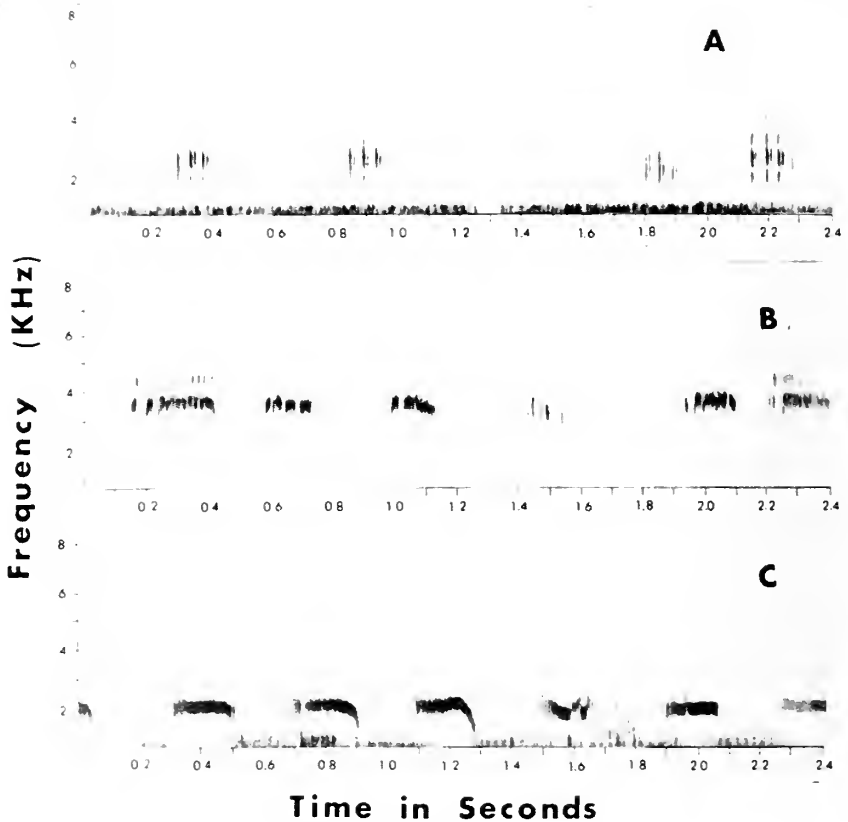


FIG. 2. Audiospectrograms of Mountain Plover calls: A, Click; B, Chatter; C, Squeal.

about 0.2 to 0.3 sec in duration, and the interval between them ranges from 0.1 to 0.4 sec. A harmonic band is present between 4.0 to 5.0 KHz on some of the calls.

Squeal Call.—Frequently when I approached a nest or brood, the attending adult would perform intense injury-feigning displays: sometimes these displays were accompanied by this call (Fig. 2C). The call is a prolonged series of notes which, both in terms of frequency and tempo, remind me of the distress squeals produced by a cottontail rabbit (*Sylvilagus floridanus*) on a commercial predator-calling record. The notes recorded by me show much variability, with a frequency between 1.0 to 2.5 KHz. Some notes are at a constant frequency, but others terminate with a definite drop in frequency. The duration between notes ranges from 0.15 to 0.2 sec. Weakly-developed harmonic elements are present.

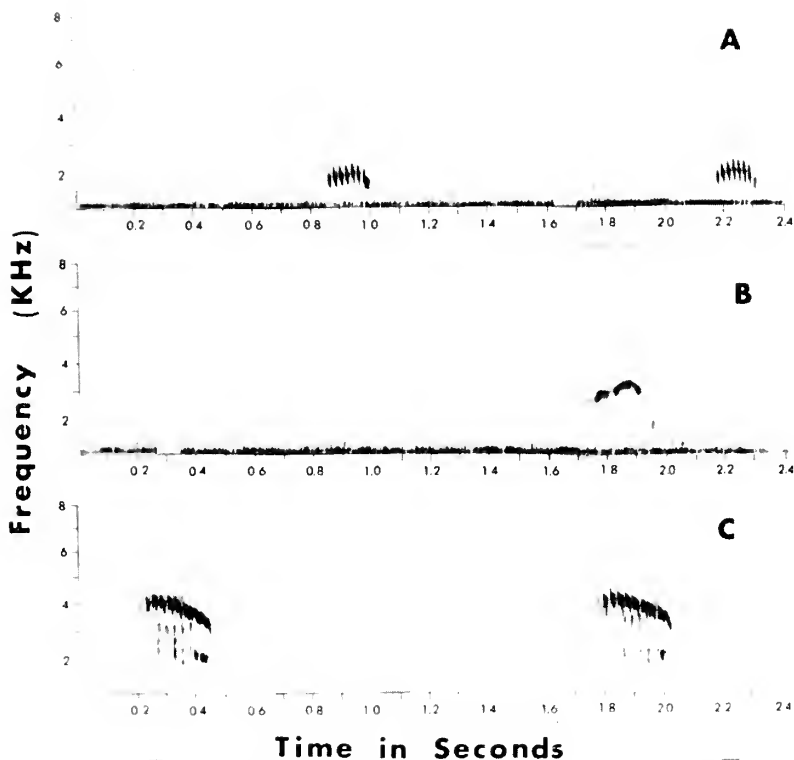


FIG. 3. Audiospectrograms of Mountain Plover calls: A, Brood; B, Peeping; C, Chick.

Brood Call.—On three occasions, by placing a microphone near a brood, I was able to record a low, guttural call (Fig. 3A) uttered by an adult as the chicks moved under it to be brooded. Although I could see the adult's throat moving as it called, I never heard the call. On one of these occasions I was within 25 m of the adult. The calls recorded by me have a frequency between 1.0 to 2.5 KHz. The duration of a call is about 0.15 sec, and the interval between calls is about 1.2 sec. I detected no harmonics on my audiospectrograms.

Peeping "Call".—Peeping sounds (Fig. 3B) could be heard in eggs up to three days prior to hatching, although they may not represent vocalizations. These sounds are quite different from the calls of newly hatched chicks. The peeping has a frequency between 2.5 to 3.5 KHz, with a fundamental frequency at about 3.0 KHz. The duration of a peep is about 0.2 sec, but I lack data on the interval between peeps. I detected no harmonics on my audiospectrograms.

Chick Call.—When held, newly hatched chicks would usually utter a rather loud call (Fig. 3C). Upon hearing this call the attending adult frequently responded by coming closer to me. The calls have a frequency between 2.0 to 4.5 KHz. with a fundamental frequency at about 4.0 KHz. The duration of a call is about 0.3 sec. I only have one continuous recording containing two calls, and the interval between the two calls is about 1.3 sec. I detected no harmonics on my audiospectrograms.

Although the above are the only calls that I have heard or recorded, I suspect that future study will show that some of these calls are given in other contexts or additional calls exist. For instance, when a male mounts a female prior to coition, his throat moves constantly, and he may be uttering sounds.

DISCUSSION

The Mountain Plover has been known to science since 1837, when it was first described by Townsend—interestingly enough—as *Charadrius montanus*. Perhaps the earliest report on the species' vocalizations was that of Elliot Coues (1874): in fact, his account has been among the most frequently cited of any in the intervening hundred years (e.g. Dawson, 1923; Bent, 1929). Subsequent authors have added bits and pieces to the vocal record of the species, and I would like to attempt to relate the published record to what I have found. In addition, I shall discuss function and other aspects of the vocalizations of the Mountain Plover.

Speaking of wintering flocks of these plovers near Los Angeles, California, Coues (op. cit.) says that "their notes are rather peculiar, as compared with those of our other plovers, according to circumstances." He goes on to describe "a low and rather pleasing whistle, though in a somewhat drawling or rather lisping tone," as being given by feeding birds considered by him to be undisturbed. Going on, he states that his "note changes to a louder and higher one, sometimes sounding harshly," but he does not mention the context surrounding the change. Conceivably, these could be the Tu-lup and Ke-op Calls recorded by me, and which I regard as alarm notes. Coues may also have been referring to the Kip Call, which I suspect is an additional alarm note, perhaps confined to flushing birds or those in flight.

Palmer (1967) has referred to chattering calls as given by this species, especially at the nest. These calls would appear to be one or both of the aggressive notes that I recorded, i.e. the Clicking and Chatter Calls. Perhaps these notes are restricted to birds at nests, but they may be used in other contexts as well. From my observations, the Clicking Call is low intensity and the Chatter Call is high intensity aggression.

Also aggressive in tendency is the Wee-wee Call, which I found used in

hostile and in territorial advertisement displays. This call is the most frequently heard during the prenesting and early nesting periods; in fact, if a Mountain Plover is heard calling in the distance, the Wee-wee Call is usually the call being given. This call is also used by birds in fall flocks, and there it probably also reflects hostile interactions; birds still maintain their individual distances in these flocks, and aggressive displays are sometimes given. There are two literature descriptions of vocalizations of this species that I would consider to be in reference to this call. Donald G. Davis, in Bailey and Niedrach (1965), reports hearing "a spring song—usually given from the wing—which I have never seen described in print: a long-drawn series of wild, harsh whistles that could be heard half a mile away." Laun (1957) refers to a "series of short chattering-like sounds phonetically expressed as a loud whispered chit-chit . . .," and he noted that this call was given in several contexts.

The Squeal Call is not described in the literature, but it is associated with injury-feigning behavior. Many birds, including shorebirds, perform injury-feigning displays, and presumably these displays serve to draw potential predators away from the nest or brood (Armstrong, 1952; Duffy et al., 1950; Simmons, 1951; Williamson, 1948). The Squeal Call may well have evolved to reinforce injury-feigning, presumably helping to direct the attention of a potential predator toward the displaying bird. The similarity of the Squeal Call to the distress call of a small mammal may not be due to chance; Duffy et al. (op. cit.) speculate that one predominant form of injury-feigning, the "rodent run," owes its biological success to its semblance of a small mammal running away. Interestingly, a call is also given during injury-feigning by the Purple Sandpiper (*Calidris maritima*) (Bengston, 1970) and the Spotted Sandpiper (*Actitis macularia*) (Oring and Knudson, 1972).

The Mooing and Chert Calls also appear undescribed in the literature; both obviously have a courtship function. The Chert Call may represent an invitation to copulate, and like the Mooing Call is given almost invariably by the male. The only exception, as already mentioned, was an instance in which a female gave a Mooing Call in response to displaying (Bowling Display) by a male.

In regard to the vocalization of the Mountain Plover with young, Bailey (1928) has reported the experience of J. Stokely Ligon. The latter heard a female with a brood give "a low call," at which the young scattered away from her and the observer. After the observer withdrew to a distance of perhaps 40 feet and into an automobile, "the mother began to quiet the young with the 'notes of ease' and they soon gathered around her." From this account, it would appear that two sets of calls were used, one to scatter the

young (perhaps the Tu-lup or Ke-op Call), and one to attract them (perhaps the Brood Call). As I have mentioned earlier, at 25 m the Brood Call was not audible to me (I have normal hearing), but at 12 to 13 m what appears to have been this call was audible to Ligon. There is the obvious advantage to low audibility in this type of call, in that the young are always near the attending adult, and any extra loudness would accomplish little, other than possibly altering predators to the presence of the young.

The Chick Call appears to be the location and/or distress note of the young and it may well persist until they are several days or even weeks old. This call is probably the equivalent of that in the young in many precocial species, including in Charadriiformes as well as in other orders of birds. The Peeping "Call" might function to synchronize hatching, as in Bobwhite Quail (*Colinus virginianus*) (Vince, 1964), or otherwise serve some chick-parent communication function. Peeping noises in the egg have also been reported for the Killdeer (*Charadrius vociferus*) (Davis, 1943), the Little Ringed Plover (*Charadrius dubius*) (Simmons, 1953), the European Golden Plover (*Pluvialis apricaria*) (Bannerman, 1961), and the Dotterel (*Eudromias morinellus*) (Nethersole-Thompson, 1973).

SUMMARY

Nine calls of the adult Mountain Plover, one chick call, and noises emitted from the egg are described. Tentative interpretations are made regarding the motivation and/or function of some of these calls. Of special interest is the speculation that one call may have evolved to enhance the effectiveness of injury-feigning behavior. A comparison between Mountain Plover vocalizations reported in the literature and those recorded in my study is made.

ACKNOWLEDGMENTS

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HYBRIDIZATION IN GROSBEAKS (*PHEUCTICUS*) IN NORTH DAKOTA

ROGER L. KROODSMA

Rose-breasted and Black-headed grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*) are complementary species that breed in eastern and western North America, respectively. Their breeding ranges overlap in the Great Plains where hybridization occurs. West (1962) described the hybridization mainly in Nebraska, and Anderson and Daugherty (1974) in South Dakota. Because very little work had been done in the more northern Plains, I began collecting grosbeaks in 1966 in North Dakota. This paper describes grosbeak hybridization in North Dakota, and compares it with that in more southern areas and in other species in the Plains. A "hybrid" as defined in this paper is any bird that is believed to have any combination of *P. ludovicianus* and *P. melanocephalus* genes, and "hybridization" is any mating involving genes of both species.

MATERIALS AND METHODS

During June and early July of 1966-1968 I collected 21 subadult and 27 adult *P. ludovicianus*-like males, 15 subadult and 35 adult *P. melanocephalus*-like males, 2 phenotypically medial hybrid males, and 12 adult female and 9 immature *P. melanocephalus*-like birds. Birds were collected as randomly as possible at each collecting locality, so that the proportions of the different phenotypes in each sample would hopefully approximate that in each population. The specimens are housed in the North Dakota State University Vertebrate Museum.

The specimens were scored according to a hybrid index system (Table 1) that includes four pairs of colors: rose vs. brown, rose vs. yellow, black vs. brown, and white vs. brown. Scores for phenotypically pure *P. ludovicianus* are "0" (0 + 0 + 0 + 0 + 0) and for *P. melanocephalus* are "20" (4 + 4 + 4 + 4 + 4). Relatively invariable characters were used in the index system so that specimens from extreme eastern and western North America (here assumed to be phenotypically and genetically pure) were indexed as "pure" (i.e. scores "0" and "20"). This assumption should be valid because hybridization between grosbeaks as described by West (1962) seems to be confined to a zone about 200 miles wide in the Plains. Anderson and Daugherty (1974), with a hybrid index system different from the one used in this paper, reported "hybrid" birds in extreme eastern and western populations; however, they regarded those birds as individual variations of the typical pure grosbeak phenotypes, rather than resulting from hybridization. According to the index system in this paper, specimens having scores of 1-19 would be judged to be hybrids. Back color could have been used in the index system, with pure black representing *P. ludovicianus* and black with broad brown streaks representing *P. melanocephalus*. It was not used because the back feathers with brown streaks of the winter plumage of *P. ludovicianus* are not always molted before the breeding season (pers. obs.), and therefore some pure *P. ludovicianus* would have received scores greater

TABLE 1
HYBRID INDEX FOR MALE GROSBEAKS (*PHEUCTICUS*)

| Character | Description | |
|--|--|---|
| Upper breast | Rose, as in Rose-breasted Grosbeak | 0 |
| | Salmon pink | 1 |
| | Intermediate between rose and brown | 2 |
| | Brown with tinge of rose | 3 |
| | Brown, as in Black-headed Grosbeak | 4 |
| Medial upper abdomen and wing linings | Rose, as in Rose-breasted Grosbeak | 0 |
| | Salmon pink | 1 |
| | Intermediate between rose and yellow (orange) | 2 |
| | Bright yellow with tinge of orange | 3 |
| Nape and crown stripes | Bright yellow, as in Black-headed Grosbeak | 4 |
| | Black, as in Rose-breasted Grosbeak | 0 |
| | Mostly black, with a few brown feathers | 1 |
| | Half black, half brown | 2 |
| | Brown with much black spotting | 3 |
| Lateral upper abdomen; rump | Brown with little or no black spotting, as in Black-headed Grosbeak | 4 |
| | White, as in Rose-breasted Grosbeak | 0 |
| | Traces of buff | 1 |
| | Half brown, half white | 2 |
| | Traces of white | 3 |
| | Brown, as in Black-headed Grosbeak | 4 |

than "0" (see Dwight, 1900, and West, 1962, for descriptions of molt sequence in *P. ludovicianus*).

Although both adult and subadult males were scored by the same index system, some exceptions in scoring were made for subadults. Nuptial-plumaged subadult *P. ludovicianus* often have brown edges on feathers of the back, black and brown rumps, and variable amounts of buff on mostly white abdomens. Because these characters are difficult to distinguish from hybrid characters, it would seem best to place more emphasis on scores of adults. In this study the characters described above in subadult *P. ludovicianus* were given scores of "0". This probably did not significantly bias hybrid index scores toward "0", because hybridization was infrequent as indicated by the scarcity of adult male hybrids (see below).

To provide further comparison of hybrid and pure grosbeaks, several standard measurements were taken as described by Pettingill (1970); bill length was measured from the anterior edge of a nostril to the tip of the upper mandible.

RESULTS

Distribution.—The ranges of the two grosbeak species in North Dakota are separated by the prairie-pothole country between the Missouri River to the southwest and the Souris, James, and Sheyenne Rivers to the northeast

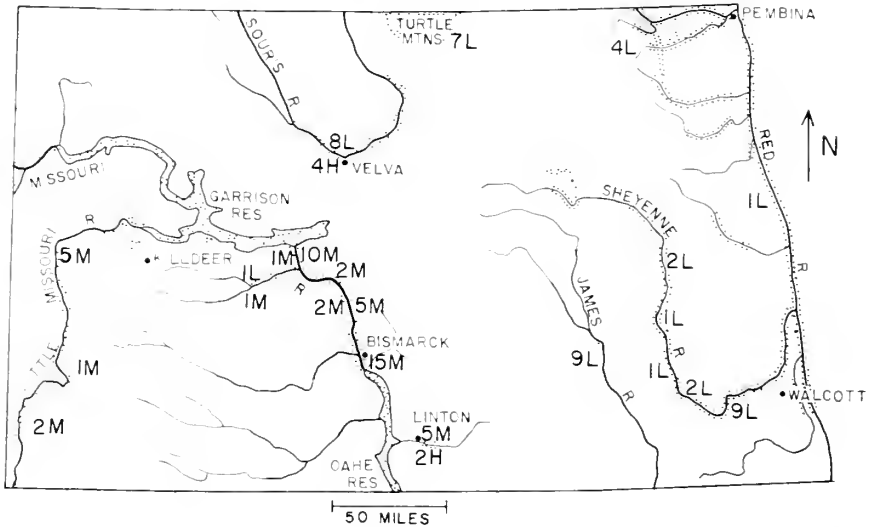


FIG. 1. Locality records of subadult and adult male grosbeaks collected in North Dakota during 1966–1968. L = *Pheucticus ludovicianus*, M = *P. melanocephalus*, and H = hybrid. The number preceding each letter is the number of specimens. Grosbeak habitat or deciduous forest is indicated by dots (except those showing reservoirs), as given by U.S. Geological Survey maps (1:250,000 series) with green forest overprint.

(Fig. 1). Upland forests and streams with riparian forests are virtually absent from this prairie country. Although some tree plantings exist in the area, grosbeaks do not utilize these appreciably as do orioles (*Icterus*) and flickers (*Colaptes*), which are forms that also hybridize in North Dakota.

Elsewhere in North Dakota, woodlands and forests along all the major streams and rivers support grosbeaks. Upland forests where grosbeaks are common are in the Killdeer Mountains (9 miles northwest of Killdeer), in the Turtle Mountains in north-central North Dakota, and in the Pembina Hills west of Pembina in the northeast. The forests consist principally of American elm (*Ulmus americana*), boxelder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and burr oak (*Quercus macrocarpa*). Plains cottonwood (*Populus sargentii*) woodlands occur along the Missouri and Little Missouri Rivers. Aspen (*Populus tremuloides*) stands predominate in the Turtle Mountains. *P. ludovicianus* were most abundant in woodlands of elm, ash, boxelder, and basswood (*Tilia americana*) along the Sheyenne River west of Walcott, and in woodlands mostly of elm along the Souris River just west of Velva. *P. melanocephalus* were most abundant in cottonwood woodlands along the Missouri River between the Garrison (Lake Sakakawea) and Oahe reservoirs.

TABLE 2
SCORES OF SUBADULT AND ADULT MALE GROSBEEKS (*PHEUCTICUS*) FROM
NORTH DAKOTA¹

| | Upper breast | Medial abdomen and wing | Nape and crown | Lateral abdomen | Rump | Average total score |
|--|-----------------|-------------------------------|----------------------|--------------------|------|---------------------------|
| <i>P. ludovicianus</i> (45) | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>P. ludovicianus</i> -like hybrids (3) | 1 | 1 | 0 | 0 | 0 | 2 |
| Medial hybrids (2) | 2 & 3 | 2 | 2 | 2 | 2 | 10.5 |
| <i>P. melanocephalus</i> -like hybrid (1) | 4 | 4 | 4 | 3 | 4 | 19 |
| <i>P. melanocephalus</i> (49) | 4 | 4 | 4 | 4 | 4 | 20 |

¹Numbers of birds are in parentheses.

Hybridization.—Only six of 100 males collected in North Dakota were hybrids, as judged from their hybrid index scores. These occurred only along Beaver Creek near Linton and along the Souris River (Fig. 1). Two very similar hybrids collected along Beaver Creek and the Souris River were phenotypically medial, with scores of 10 and 11 (Table 2). Three hybrids collected along the Souris River west of Velva were more similar to *P. ludovicianus* with scores of 2. One possible hybrid collected along Beaver Creek was similar to *P. melanocephalus*, with a score of 19. The 12 adult females and nine immatures were collected from the mainly *P. melanocephalus* populations from Beaver Creek to the Garrison Reservoir. One immature and three females, although generally similar to *P. melanocephalus*, had orange underwing linings. Because female and immature *P. melanocephalus* have yellow underwing linings, these four specimens are apparently hybrids. Females and immatures thus included a greater proportion of hybrids than did males, but the small sample size prohibits any generalizations. All other specimens from North Dakota, including 94 males, were phenotypically pure, with scores of 0 or 20.

During 1969 and 1971 I made additional observations on grosbeaks during behavioral experiments, in which a total of 116 territorial males were attracted to mounted specimens by recorded songs (Kroodsma, 1974). I was usually able to observe carefully each of these birds (with 8 × 30 binoculars) for a few minutes at nearly horizontal distances of 30–60 feet. I saw no obvious hybrids in 44 *P. melanocephalus* along the Missouri River south of Bismarck—where I saw one apparently pure *P. ludovicianus*, and no obvious hybrids in 47 *P. ludovicianus* along the Sheyenne River west of Walcott.

TABLE 3
MEANS \pm ONE STANDARD DEVIATION OF MEASUREMENTS (IN MM)
OF MALE GROSBEAKS IN NORTH DAKOTA¹

| | Rose-breasted Grosbeak | | Black-headed Grosbeak | |
|--------------|------------------------|-----------------|-----------------------|-----------------|
| | Subadult (21) | Adult (27) | Subadult (13) | Adult (36) |
| Wing | 98.7 \pm 1.8 | 101.8 \pm 2.4 | 100.7 \pm 2.2 | 103.1 \pm 2.0 |
| Tail | 72.2 \pm 2.4 | 73.8 \pm 2.6 | 76.4 \pm 2.3 | 78.2 \pm 2.3 |
| Bill | 12.3 \pm 0.6 | 12.3 \pm 0.4 | 12.6 \pm 0.4 | 12.8 \pm 0.5 |
| Tarsus | 22.2 \pm 0.6 | 22.6 \pm 0.8 | 23.8 \pm 0.9 | 23.6 \pm 0.9 |
| Total length | 207.6 \pm 5.1 | 209.4 \pm 4.3 | 212.2 \pm 4.9 | 214.0 \pm 4.5 |
| Weight | 45.5 \pm 3.6 | 44.6 \pm 2.5 | 46.0 \pm 1.8 | 46.2 \pm 3.0 |

¹ Sample sizes are in parentheses.

Along the Souris River I saw 20 apparently pure *P. ludovicianus*, three *P. ludovicianus*-like hybrids, and one hybrid very similar to the two phenotypically medial hybrids described above. The *P. ludovicianus*-like hybrids included one with an entirely pale yellow breast and two with salmon-pink breasts with brown sides. The medial hybrid had an orange and brown breast and brown collar.

Measurements.—Subadult males were smaller than adult males in all measurements in *P. ludovicianus* except weight and in *P. melanocephalus* in tarsus (Table 3): however, only differences between wing and tail lengths in each species were significant ($P < 0.05$ by analysis of variance). Subadults and adults should therefore not be pooled during comparisons of these two size characters. For each respective age group, *P. melanocephalus* averaged larger than *P. ludovicianus* in all characters. The differences were significant ($P < 0.05$ by analysis of variance) for all except bill and weight of subadults. Thus in North Dakota the two species are distinct in size characteristics. West (1962) did not find such degrees of differences, possibly because he apparently pooled adults and subadults. Measurements of the small sample of hybrids did not show any noteworthy trend toward intermediacy.

DISCUSSION

Hybridization between grosbeaks is much less frequent in North Dakota than in South Dakota and Nebraska, and no hybrid zone or zone of overlap and hybridization (as defined by Short, 1969) exists. Hybridization in North Dakota may be less frequent because: 1. there are no rivers with riparian

woodlands to allow dispersal along the relatively treeless country between the breeding ranges of the two species; 2, relatively dense populations of grosbeaks on either side of the treeless country may quickly swamp phenotypic evidence of the infrequent hybridization; and 3, large reservoirs on the Missouri River may inhibit northwestward dispersal by *P. ludovicianus* into the range of *P. melanocephalus* along the Missouri River in North Dakota. Under these conditions contact between the two species and hybridization in North Dakota will probably not increase significantly.

Hybridization in grosbeaks is less extensive than that in the North American orioles and flickers as described by Sibley and Short (1964), Short (1965), and Anderson (1971). This may be true because the two grosbeak species: 1, have narrower habitat requirements and consequently less contact in the Plains; 2, mate assortatively—as indicated by West (1962) and Anderson and Daugherty (1974); 3, exhibit sufficiently large phenotypic differences in males that allow species-specific identification by males (Kroodsmä, 1974); and 4, may have greater physiological differences. An example of the last is an apparent difference in molt, which—to my knowledge—has not been previously noted in the literature. In *P. melanocephalus* the feathers were always very worn and pointed in spring and summer specimens. In contrast, the feathers of *P. ludovicianus* had smooth unworn margins and rounded tips. Thus *P. melanocephalus* apparently lacks a prenuptial (prealternate) molt, while *P. ludovicianus*—as also stated by Dwight (1900)—has a prenuptial molt of the body feathers. Flickers (*C. auratus auratus* and *C. a. cafer*) and orioles (*I. galbula galbula* and *I. g. bullockii*) apparently show no such differences in molt (pers. obs.). A difference in molt in the two grosbeak species could indicate deep-seated physiological differences, which could in turn relate to reduced viability and fertility of hybrids. Hybrid females apparently lay more nonviable eggs than do pure females (Anderson and Daugherty, 1974).

All hybrids collected in this study showed a partial prenuptial molt of the body feathers, as indicated by the presence of both new and old feathers on the backs. In *P. ludovicianus*-like birds it would be desirable to know whether the presence of worn brown feathers on the backs results from hybridization with *P. melanocephalus* or from a delayed prenuptial molt as in *P. ludovicianus* (see methods section). This might be determined by comparing allopatric and hybridizing populations with respect to the proportion of birds that do not completely molt the body feathers of the winter plumage before the breeding season. The extent of the prenuptial molt could be inversely related to the frequency of *P. melanocephalus* genes, if the molt differences outlined above are constant in the two species.

SUMMARY

During June and July of 1966-1968, 100 male grosbeaks (*Pheucticus*) were randomly collected in North Dakota. The hybrids consisted of three *P. ludovicianus*-like, two phenotypically medial, and one *P. melanocephalus*-like hybrids, these occurring along Beaver Creek near Linton and along the Souris River. Hybridization is thus less frequent than in the more southern Great Plains. The breeding ranges of the two species in North Dakota are separated by relatively treeless country between the Missouri River and other rivers to the east. Invasion of each other's range and subsequent hybridization are apparently limited by this treeless country and large reservoirs on the Missouri River. Compared with orioles (*Icterus*) and flickers (*Colaptes*), grosbeaks hybridize less frequently, possibly because of greater phenotypic and physiological (e.g. molt) differences, narrower habitat requirements, and assortative mating. Adult males of the two species were significantly different in all six size characters measured.

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ANALYSIS AND COMPARISON OF GAITS IN WHISTLING DUCKS (*DENDROCYGNA*)

M. KENT RYLANDER AND ERIC G. BOLEN

In this paper we analyze the kinetics of the walking gait of four species of whistling or tree duck: *Dendrocygna arcuata*, *D. autumnalis*, *D. bicolor*, and *D. eytoni*. Our aim was to record and compare the gaits of these species and to relate our findings to such features as behavior, habitat usage, and evolution of the species. Closely related species are often useful for studies of adaptive radiation, as evidenced by Lack's (1947) extensive study of insular birds. Whistling ducks provide a wide-ranging group of species for such study, as we have already demonstrated in anatomical-ecological studies of North American *D. autumnalis* and *D. bicolor* (Rylander and Bolen, 1970). The species chosen for the present study are among the better-known dendrocygnids, particularly in terms of habits and ecology. Finally, we include phenograms of the relationships of these species.

METHODS AND MATERIALS

We photographed walking individuals of *Dendrocygna arcuata*, *D. autumnalis*, *D. bicolor*, and *D. eytoni* with a Canon Auto Zoom 618 Super 8 camera at 48 frames per second. The birds were housed in outdoor pens at the Breckenridge Zoo, San Antonio, Texas, and the Wildfowl Trust, Slimbridge, England. Our techniques and analysis generally follow Cracraft's (1971) study of pigeon gaits. We projected film sequences with a Bell and Howell Super 8 Autoload "multi motion" projector and traced the images contained on every other frame (1/24th second).

Our sample of 16 complete strides consisted of three each from three *autumnalis* specimens, three from one *bicolor* specimen, two from a single *eytoni* specimen, and two from a single *arcuata* specimen. These sample strides were selected from a large series of strides because: 1, they were all photographed at suitable distances and angles; 2, they all involved ducks having no obvious locomotor impairments; and 3, they all were executed at about the same velocity. Minimal sampling variation can be achieved when the film sequences for gait analysis are carefully selected. An analysis of variance detected no significant differences ($P > 0.01$) between gaits of the same bird or between gaits of different birds of the same species.

We analyzed the stride through the movements at four joints: the hip joint (femur/acetabulum), the knee joint (femur/tibiotarsus), the intertarsal or ankle joint (tibiotarsus/tarsometatarsus), and the tarsometatarsal/phalangeal joint. Of these, only the movements at the tarsometatarsal/phalangeal joints lacked apparent correlation with specific types of gaits.

The angles at the hip and knee are not directly visible in the photographs. To measure them we located the femur and tibiotarsus by independently locating the acetabulum by the following two methods (Fig. 1). First, we measured the distance between the tip of the tail and the acetabulum in preserved specimens and transferred the equiv-

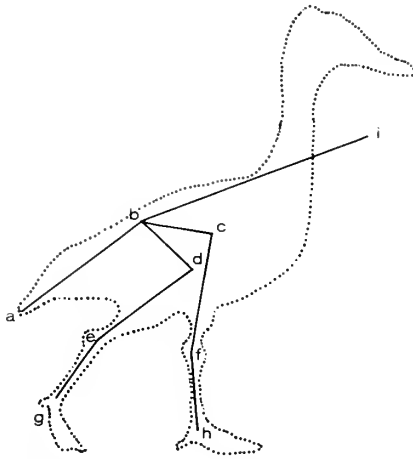


FIG. 1. Whistling duck (*Dendrocygna*) profile indicating two methods for estimating the position of the acetabulum from motion picture tracings. In one method, the distance ab , equivalent to the average tail-acetabular length on preserved specimens, is used to determine the location of the acetabulum. In a second method, if a circle is drawn having its center at d and a radius db , representing the length of the femur, and a corresponding circle having its center at c and a radius cb is drawn on a tracing of the duck at a later point in the stride, then when the two tracings are superimposed, the acetabulum is located at the point where the two circles intersect (i.e. at b). See text for further explanation. This figure also illustrates the angle formed by the anterior ilium and the femur (angle cbi), which necessarily increases when the posture assumes a more vertical bearing in *D. eytoni* and *D. autumnalis*.

alent of this measurement to the tracings. Second, we superimposed two tracings made from frames that showed a duck in two different parts of the same stride. During the time interval between the two frames, the tarsometatarsus changed position (represented by two separate lines (de and cf) on the superimposed tracings). Using the angles at the intertarsal joint (deg and cfh), we drew the tibiotarsus in its two positions; the equivalent length of this bone (calculated from known skeletal proportions and tarsometatarsal length) enabled us to locate its proximal end (the knee joint: c and d). We used the equivalent length of the femur as the radius of two circles centered on the two knee joint positions (bc and bd). The intersection of these circles indicated the location of the acetabulum (b).

In both methods, we necessarily relied on bone measurements from specimens other than those we photographed. Errors attributable to the small variation in bone lengths were calculated at less than two degrees at each of the joints; these do not affect the validity of our results. Likewise, errors attributable to variations in the calculated position of the acetabulum were less than one degree at the joint. Although it is preferable to obtain bone measurements from the subjects actually photographed, we believe our method of analysis is well suited for studying gaits of wild animals on film.

Computations for the phenograms were done using the NT-SYS package of computer programs for numerical taxonomy obtained from F. James Rohlf, State University of

New York at Stoney Brook. The characters used were as follows: 1, plume development; 2, tongue structure; 3, bill spotting; 4, bill coloration; 5, white on wing; 6, patch on wing; 7, foot color; 8, neck striated; 9, markings distinct on downy plumage; 10, downy with bands (not spots); 11, downy plumage base color yellow; 12, tail length; 13, iris color; 14, bill length (relative); 15, wing size; 16, abdominal markings; 17, specialized primaries; 18, tail coverts white-buff; 19, eye ring; 20, spotted breast; 21, voice; 22, occipital tufts; 23, black neck stripe; 24, post-copulatory display; 25, body feathers with spotted tips; 26, throat posture; 27, mutual nibbling; 28, tracheal structure; 29, nocturnal behavior; 30, egg color; 31, egg size; 32, nest in trees; 33, nest over water; 34, perch commonly; 35, nests far from water with regularity; 36, short tarsus to mid-toe ratio; 37, flared pelvis; 38, curved femur; 39, vertical posture; 40, horizontal posture; 41, walking gait; 42, nail shape; 43, lamellae number; 44, bill area; 45, bill epidermis; 46, feeding behavior; 47, upper bill cavity; 48, nares near bill tip; 49, lamellae shape; 50, neck muscles; 51, equilibrium (auditory lobe); 52, equilibrium (semicircular canal); 53, cerebral axis; 54, parallel bill sides; 55, paraglossal size; 56, ceratohyal size; 57, integument lining of maxilla; 58, forehead-bill profile; 59, optic tectum; and 60, semilunar ganglion.

FUNCTIONAL MORPHOLOGY

Although we compared numerous detailed characters of the stride in the four species, only angular displacements at the hip joint (angle *cbi*) reflected an obvious association with differences in gaits (Fig. 2). These differences separate the four species into two well-defined groups: 1, *D. bicolor* and *D. arcuata*; and 2, *D. autumnalis* and *D. eytoni*. The former species initiate

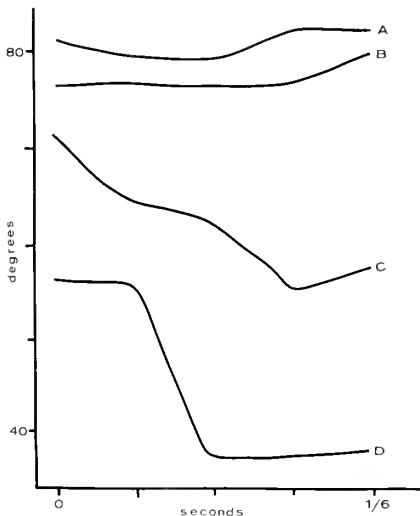


FIG. 2. Sample angular displacements at the hip and knee joints during the first one-fourth of a stride. A, *D. autumnalis*; B, *D. eytoni*; C, *D. bicolor*; D, *D. arcuata*.

TABLE 1

EXTENSION OF KNEE AND ANKLE JOINTS COMBINED (IN DEGREES) AT 1/24 SECOND INTERVALS DURING FIRST HALF OF A STRIDE IN WHISTLING DUCKS (*DENDROCYGNA*).

| Time (seconds) ² | Angle <i>bef</i> + Angle <i>cfh</i> ¹ | | | |
|--|--|------------------|-------------------|-------------------|
| | <i>D. autumnalis</i> | <i>D. eytoni</i> | <i>D. bicolor</i> | <i>D. arcuata</i> |
| 0 | 266 | 287 | 211 | 237 |
| 1/24 | 220 | 222 | 211 | 181 |
| 2/24 | 181 | 180 | 129 | 159 |
| 3/24 | 135 | 143 | 118 | 113 |
| 4/24 | 165 | 139 | 144 | 129 |
| 5/24 | 207 | 186 | 185 | 161 |
| 6/24 | 198 | 298 | 237 | 240 |
| 7/24 | 243 | 302 | 237 | 240 |
| Total degree seconds during first half of stride | 59.6 | 57.0 | 46.4 | 48.4 |

¹ See Fig. 1 for illustration of angles used in this analysis.

² The total number of degree seconds for this half of a stride was derived by graphing the numbers in the table and determining the area under the curves.

³ All four specimens completed the half stride within 1/24 of a second of each other.

their stride with a more horizontally aligned body, as measured by a smaller hip angle (*cbi*), than do the others; moreover, during the first one-fourth of the stride, this angle becomes significantly less than that in the second pair. (We are here defining a "stride" as the movement of one leg from the moment the foot leaves the ground until it next leaves the ground). We found no significant differences between the pairs with regard to hip movements during the remainder of the stride, although we suspect that larger samples of ducks photographed at higher speeds under controlled conditions may reveal less obvious gait characters of importance.

When the sum of angles *bef* and *cfh* are graphed for the first half of the stride, the areas enclosed by the curves for *autumnalis* and *eytoni* are greater than for *bicolor* and *arcuata* (Table 1). This indicates that *autumnalis* and *eytoni* carry their legs in a more extended condition during this time. The degree of extension of the knee and ankle joints was about the same for all four species during the second half of the stride, when all birds support themselves on a relatively immobile leg as the other leg advances.

The two pairs are also separable on the basis of posture: we consider this closely related to locomotion, although the nature of the relationship is not clear in every respect. *D. autumnalis* and *eytoni* have a relatively vertical posture, whereas *bicolor* and *arcuata* have a more horizontal posture (Fig.

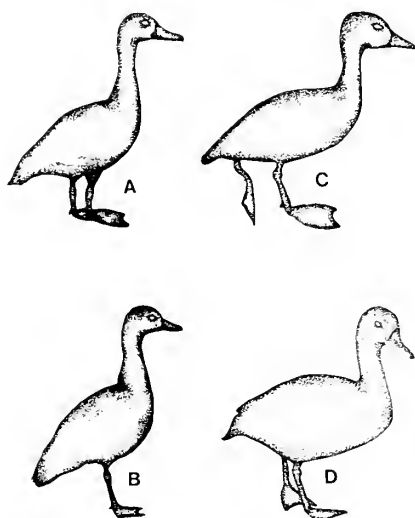


FIG. 3. Profiles of four species of whistling duck showing their characteristic postures on land (see Fig. 2 for legend of species). The profiles were drawn from photographs of living birds.

3). The vertical posture in *autumnalis* and *eytoni* is clearly a function of angle *cbi* (Fig. 1), but it is not necessarily related to the distinctions in angles *bcf* and *cfh*.

In summary, *D. bicolor* and *D. arcuata* initiate their stride and also stand more horizontally than do *D. autumnalis* and *D. eytoni*.

ECOLOGICAL RELATIONSHIPS

The following synopses provide a brief ecological comparison of the four whistling ducks. Of particular relevance to the gait and posture data are each species' walking and swimming habits, their feeding stations, and the location of their nests.

Black-bellied Whistling Duck: *D. autumnalis* is particularly adept at perching and climbing in trees (Rylander and Bolen, 1970), as well as at walking skillfully. Adults swim with their broods, but otherwise swimming is minimal after the breeding season ends: the birds instead wade in shallow water or bask on mud flats. Loafing Black-bellied Whistling Ducks commonly spar among themselves, involving a considerable amount of intense running to or from an opponent. Feeding flights take them to grassy pastures or to grain stubble, sometimes at considerable distances from water (Bolen and Forsyth, 1967). This species, unlike the others discussed, usually

ests in tree cavities at varying distances from water, although we have found some nests on the ground in heavy cover during the course of our field studies. Range: New World.

Plumed Whistling Duck: *D. eytoni* walk long distances gracefully on land but perch in trees only awkwardly and rarely: they seldom dive, except when wounded, and are slow and awkward swimmers (Frith, 1967:80). Lavery (1967) observed that the daily feeding routine starts in the later afternoon, when the birds walk and graze near their roosting sites, then fly to feeding areas elsewhere; they feed mainly on land, eating mostly grasses. This species nests on the ground in the shelter of long grass or a bush, often a mile or more from water. Range: Australia.

Wandering Whistling Duck: *D. arcuata* makes little or no use of tree perches. They are adept swimmers and feed entirely in water, taking small amounts of animal matter and various parts of aquatic plants; their foods are secured by expert and constant diving. Frith (1967:66) once watched several thousand Wandering Whistling Ducks froth the water to a boil as they swam and dove for food. It is primarily in their utilization of foods secured in relatively deep water that the Wandering Whistling Duck remains ecologically separate from the Plumed Whistling Duck throughout their sympatric ranges in Australia (Frith, 1967:88). The nest of this species is a sheltered, grasslined depression on the ground, often far from water. Range: Australia, East Indies (part), and Philippines.

Fulvous Whistling Duck: *D. bicolor* dive readily, and their large feet are structural adaptations presumably related to their swimming habits (Rylander and Bolen, 1970). This species never seems to perch in trees and seldom walks more than a short distance. Fulvous Whistling Ducks feed on the seeds of grasses and sedges common to their aquatic habitats. The species nests in aquatic habitats with dense swards of marsh grasses and other aquatic vegetation. In Louisiana, and elsewhere in North America, they often seek the cover afforded by cultivated rice (*Oryza sativa*) (Lynch, 1943; Meanley and Meanley, 1959). Cottam and Glazener (1959) regularly found nests constructed in grasses rooted in waist-deep water in Southern Texas. Range: New World, Africa, and India.

To summarize, *D. bicolor* and *arcuata* are highly aquatic in their ecology and behavior, and they are characterized by their horizontal posture (Fig. 3) and a more horizontally-initiated gait (Fig. 2, Table 1). In contrast, *D. autumnalis* and *eytoni* are less aquatic and more cursorial in their habits, and they are characterized by their more vertical posture and a less horizontally-initiated gait.

We have thus shown correlations between the functional morphology of

gaits in four closely related species and the behavioral differences that they exhibit. On these bases the four species of Whistling Ducks in this study can be grouped into two pairs, each consisting of one predominately swimming and one cursorial species. One pair, *D. autumnalis* and *bicolor* are sympatric in the New World, whereas the other, *D. eytoni* and *arcuata*, are sympatric in Australia.

PHENETIC RELATIONSHIPS

In order to elucidate possible relationships between the four species on the basis of gait, we prepared a phenogram based first on 60 characters (see Methods). Secondly, we deleted 25 of the 60 and prepared a phenogram based on 35 characters (1 through 35) that we believe have no obvious adaptive significance associated with locomotion or feeding activity. The basis on which to delete characters from the second phenogram was the belief that iris color, for example, could be logically separated from bill shape or foot size as a less than obvious feature of adaptation toward either locomoting or feeding. Hence, such characters as iris color, post-copulatory stance, and downy plumage characters were used in the second phenogram (Fig. 4, lower); such characters as lamellae shape and number, feeding behavior, foot size, and certain features of the skull (see Rylander and Bolen, 1974) were omitted as clearly adaptive.

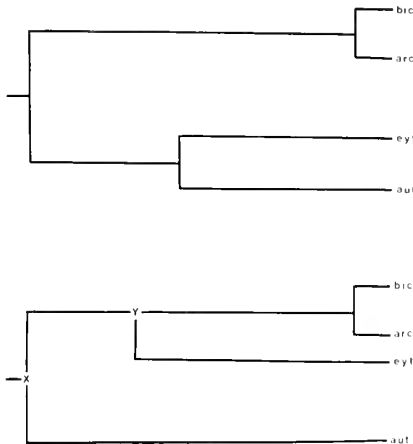


FIG. 4. Phenograms indicating distances between *D. bicolor* (*bic*), *D. arcuata* (*arc*), *D. autumnalis* (*aut*) and *D. eytoni* (*eyt*). The upper phenogram was based on 60 morphological, ecological, and behavioral characters; the lower phenogram was based on 35 of these characters that seemingly have no obvious adaptive significance (see methods section). Points of divergence are indicated by X and Y in the lower diagram.

Basically, the 60 character phenogram indicates that the two aquatic, swimming species (*D. bicolor* and *arcuata*) are more closely interrelated than are the two semiaquatic, cursorial species (*D. autumnalis* and *eytoni*). The 30 character phenogram goes on to show that *D. eytoni* is, in fact, closer to *bicolor* and *arcuata* than to *autumnalis*. The relatively great phenetic distances (Fig. 4) between *eytoni* and *autumnalis*, as well as their widely separated ranges, may be regarded as evidence that the two are not particularly closely related. Thus, their similarity in gait may well be due to parallel evolution, and we suspect that the common ancestor of each species may have had a gait like that of the *D. bicolor-arcuata* group. In other words, we postulate that the cursorial gait is derived, in the case of *D. autumnalis* and *eytoni*; thus, at least in the species of *Dendrocygna* here analyzed, the gait of swimming species may be the more primitive. If we postulate that the gait in *D. autumnalis* and *eytoni* evolved independently, then obviously this and related characters cannot be regarded as having phylogenetic value in studying the relationships of these species.

SUMMARY

The gaits of four broadly distributed species of whistling duck (*Dendrocygna*) were compared. Differences in the angular displacement were greatest at the hip joint and separated the four species into two groups: one group containing the relatively cursorial species, *D. autumnalis* and *eytoni*, and the other the predominately swimming species, *D. bicolor* and *arcuata*. The first group initiates its stride with a larger hip angle and less angular displacement than the second group. The *autumnalis-eytoni* group also assumes a more vertical posture on land than the second group. Consideration of the feeding habits of each species sharpens the ecological distinctions between the two pairs of species.

The possibility that *autumnalis* and *eytoni* evolved the same type of gait independently is suggested by phenetic analyses of the group.

ACKNOWLEDGMENTS

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TELECREX RESTUDIED: A SMALL EOCENE GUINEAFOWL

STORRS L. OLSON

In reviewing a number of the fossil species presently placed in the Rallidae, I have had occasion to examine the unique type—an incomplete femur—of *Telecrex grangeri* Wetmore (1934), described from the Upper Eocene (Irdin Manha Formation) at Chimney Butte, Shara Murun region, Inner Mongolia. Although Wetmore assigned this fossil to the Rallidae, he felt that the species was distinct enough to be placed in a separate subfamily (Telecrecinae); this he considered to be ancestral to the modern Rallinae. After apparently examining the type, Cracraft (1973b:17) assessed it as “decidedly raillike in the shape of the bone but distinct in the antero-posterior flattening of the head and shaft.” However, he suggested that Wetmore’s conclusions about its relationships to the Rallinae would have to be re-evaluated. Actually, *Telecrex* bears very little resemblance to rails, and the distinctive proximal flattening of the shaft (but not of the head, contra Cracraft) is a feature peculiar to certain of the Galliformes. Further, my comparisons show *Telecrex* to be closest to the guineafowls (Numididae), a family hitherto known only from Africa and Europe.

DISCUSSION

The type specimen of *Telecrex grangeri* (AMNH 2942) is a right femur, lacking the distal end and part of the trochanter (Fig. 1). Its measurements are: proximal width 11.6 mm, depth of head 4.2, width of shaft at midpoint 4.6, depth of shaft at midpoint 4.1, overall length (as preserved) 46.1.

Telecrex differs from all rails and agrees with the more advanced Galliformes in the flattening of the proximo-posterior portion of the shaft (so that what usually forms the lateral surface of the shaft becomes oriented almost posteriorly), in its overall proportions (a rail femur of the same thickness would be much longer), in the much greater curvature of the shaft, in the near obliteration of the pit in the head for the ligamentum teres (well-developed in the Rallidae), and in the size, shapes, and positions of the muscle scars on the proximo-lateral surface of the shaft (these scars in *Telecrex* agreeing exactly with those found in Galliformes, Fig. 2). These differences are diagnostic and serve to remove *Telecrex* from the Rallidae and place it in the Galliformes.

Within the Galliformes, the femora of the Cracidae and Megapodiidae are relatively long and slender, with the shafts less curved and not flattened, and

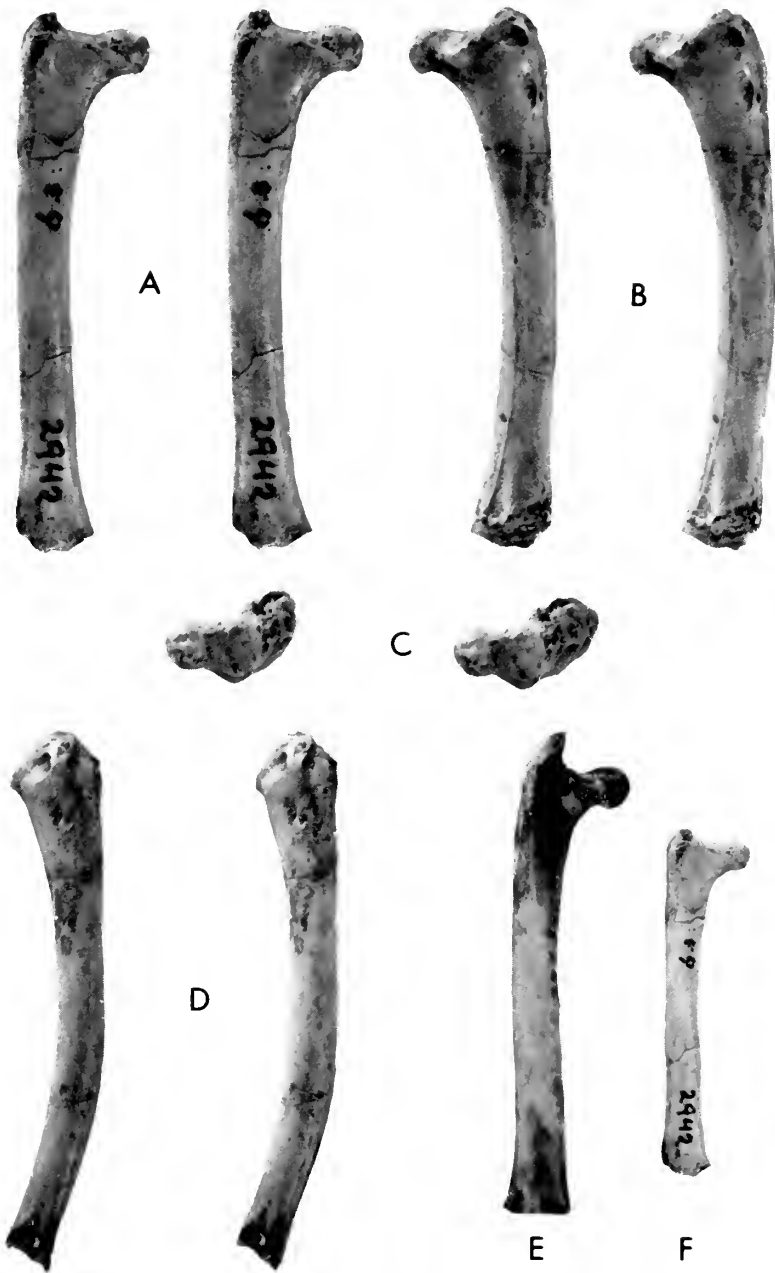


FIG. 1. *Telecrex grangeri* (Numididae), holotype femur (AMNH 2942). A-D, Stereo pairs at 1.5X; (A, anterior view; B, posterior view; C, proximal view; D, lateral view); E, femur of *Phasidus niger* (Numididae), anterior view, natural size; F, femur of *Telecrex grangeri*, anterior view at natural size for comparison.

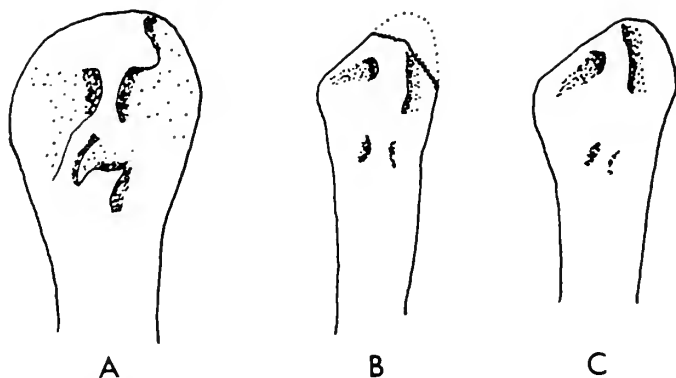


FIG. 2. Lateral views of proximal ends of femora, showing patterns of muscle scars: A, *Gallinula mortierii* (Rallidae); B, *Telecrex grangeri* (Numididae); C, *Phasidus niger* (Numididae). Not to scale.

have a deeper neck than in *Telecrex*. The Tetraonidae (and some of the Phasianidae) differ from *Telecrex* in having pneumatic foramina in the anterior face of the femur just below the trochanter, a shaft not so flattened, the neck deeper, and in lacking a ridge from the trochanter to the head. *Telecrex* differs from the Meleagrididae in its more curved shaft, less developed trochanter, and in having a wider space between the trochanter and the head.

Among the Galliformes, the femora of the Numididae and the Phasianidae are closest to that of *Telecrex*. The femur of *Telecrex* differs from that of pheasants and agrees with that of guineafowls (and particularly that of *Phasidus*) in the following particulars: in proximal view the neck is more latero-medially elongate and oriented at more of an angle to the antero-posterior plane of the bone, whereas in the Phasianidae the neck is deeper and more nearly aligned with the antero-posterior plane (Fig. 3): in proximal and anterior views the space between the trochanter and the head is wider, and there is a distinct ridge along the anterior edge of the neck that connects these two features. The shaft is wider in anterior view and thinner and more curved in lateral view. In one respect, *Telecrex* more closely resembles the Phasianidae than the Numididae—in all views the head is less distinctly set off from the neck.

In short, when compared with modern Galliformes, *Telecrex* is most similar to the Numididae, and where it differs from that group it resembles the Phasianidae. In view of the great age of *Telecrex*, it is not surprising that it does not conform precisely to the limits of modern groups. However, its greater similarity to the guineafowls is sufficient enough to permit its being placed in that group. For those that would make the Numididae only a sub-

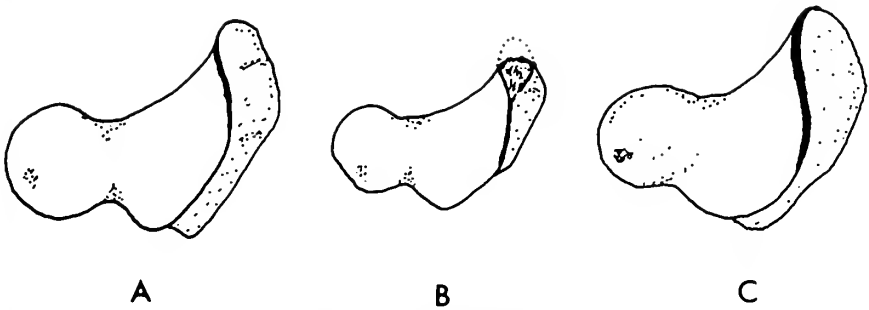


FIG. 3. Proximal views of femora: A, *Phasidus niger* (Numididae); B, *Telecrex grangeri* (Numididae); C, *Chrysolophus pictus* (Phasianidae). Not to scale.

family of the Phasianidae (e.g. Mayr and Amadon, 1951), the familial placement of *Telecrex* would present no obstacles; but I am not convinced of the wisdom of merging these two groups into a single family.

The resemblance between the femora of *Telecrex* and *Phasidus niger* is rather striking. *Phasidus* differs from *Telecrex* in having a large bulge below the posteriormost corner of the neck, making the shaft appear less flattened. This protruberance is reduced in *Numida* and *Acryllium*. The resemblance of *Telecrex* to *Phasidus* is the more interesting because the latter is the most aberrant and probably most primitive of the guineafowls and is confined to the forests of Lower Guinea. I have already called attention to the relict nature of elements of the avifauna of this region (Olson, 1973).

Telecrex was considerably smaller than the smallest of modern guineafowls (*Phasidus*), possibly indicating a greater diversity in the Numididae in the past—as was apparently true also in the Meleagrididae (Olson and Farrand, 1974).

At present the Numididae are confined to Africa, the only extralimital occurrences being Pleistocene and prehistoric remains of *Numida meleagris* from Germany, Czechoslovakia, and Hungary (Brodkorb, 1964). The presence in the Eocene of central Asia of the numidid-like *Telecrex*, which appears to be the earliest Old World galliform yet recognized, may indicate that the guineafowls are not African in origin. There is as yet, however, no reason to believe that they originated in North America, as Cracraft (1973a: 154) has strangely suggested. *Telecrex* provides an indication that forms referable to the more advanced groups of the Galliformes had already evolved by the late Eocene.

SUMMARY

Telecrex grangeri, from the Upper Eocene of Mongolia, is removed from the Rallidae and placed in the Numididae (guineafowls) of the order Galliformes. It was smaller

than any of the modern guineafowls and appears to be the earliest Old World galliform yet known. *Telecrex* suggests that the more advanced groups of Galliformes evolved early in the Tertiary and that the Numididae may not have originated in Africa.

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ANOTHER OLD WORLD VULTURE FROM THE NEW WORLD

ALAN FEDUCCIA

The Old World vultures (Accipitridae: Aegypiinae) comprise a group of raptors presently confined to Africa and Eurasia. One of the great surprises in avian paleozoogeography was the discovery of fossils of such vultures in the Tertiary and Quaternary of North America. Aegypiine vultures are very likely derived from an eagle-like ancestor and are placed in the same family and order (Falconiformes) as living hawks and eagles. The New World vultures (Falconiformes: Cathartidae), presently confined to North and South America (first known from the Eocene of North America), are not closely allied to their Old World counterparts. Although placed in the same order, cathartid vultures are rather distantly related to other accipitriforms. In fact, some workers (see Ligon, 1967) believe that they may be more closely related to storks and their allies (Ciconiiformes).

The first vultures to be described as definite aegypiines from North America were *Neogyps errans* and *Neophrontops americanus*, both from the Pleistocene Rancho La Brea and named by the late Loye Miller (1916). Years after describing them, Miller (Miller and DeMay, 1942:95) admitted that, “. . . announcement was withheld for two years because of the wide geographic separation from other members of the Old World vulture group.” Since then an even earlier aegypiine, originally described as a cathartid, *Cathartes umbrosus* (Cope, 1874), has come to light in North America (Howard, 1932:70); this Pliocene species is presently called *Palaeoborus umbrosus* (Cope). Old World vultures have now been found commonly in the Pleistocene of California, and additional species representing three genera are known from the Miocene, Pliocene, and Pleistocene of North America, including Mexico (Table 1).

The species described herein represents a late Pliocene occurrence of the genus *Neophrontops*, and the first Old World vulture recorded from Idaho. It is described below, as

Neophrontops slaughteri, sp. nov.

Holotype.—Distal end of left tibiotarsus, University of Michigan Museum of Paleontology no. V52265 (Fig. 1); no other material seen.

Horizon and locality.—Late Pliocene Hagerman local fauna (locality 540) of the Glens Ferry Formation (Malde and Powers, 1962), Twin Falls

TABLE 1
THE FOSSIL OLD WORLD VULTURES KNOWN FROM THE NEW WORLD¹

| Species | Range | Age |
|--|--|---------------------------|
| <i>Palaeoborus rosatus</i> A. H. Miller & Compton | South Dakota | Lower Miocene |
| <i>Palaeoborus howardae</i> Wetmore | Nebraska | Middle Miocene |
| <i>Palaeoborus umbrosus</i> (Cope) | New Mexico | Lower Pliocene |
| <i>Neophrontops vetustus</i> Wetmore | Nebraska | Middle Miocene |
| <i>Neophrontops dakotensis</i> Compton | South Dakota, Oregon | Lower and middle Pliocene |
| <i>Neophrontops slaughteri</i> Feduccia | Idaho | Upper Pliocene |
| <i>Neophrontops vallecitoensis</i> Howard | California | Middle Pleistocene |
| <i>Neophrontops americanus</i> L. Miller | California, New Mexico (Howard, 1971), Mexico | Upper Pleistocene |
| <i>Neogyps errans</i> L. Miller | California, Nevada, Mexico | Upper Pleistocene |

¹ Primarily from Brodkorb (1964).

County, Idaho. Although the Glens Ferry Formation was deposited from late Pliocene (early Blancan) to early Pleistocene (latest Blancan), the deposits in the vicinity of Hagerman are late Pliocene (see Hibbard et al., 1965; Zakrzewski, 1969; and Bjork, 1970). There is a potassium argon date of 3.48 ± 0.27 million years B. P. for the horizon (Evernden et al., 1964).

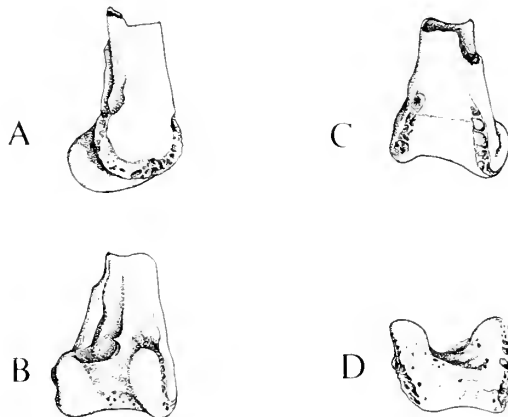


FIG. 1. Holotype tibiotarsus (UMMP V52265) of *Neophrontops slaughteri* (actual length, 21.7 mm). A, external condyle; B, posterior view; C, anterior view; D, distal end. Approximately natural size.

Etymology.—The specific name is in honor of Bob H. Slaughter, Director, Shuler Museum of Paleontology, Southern Methodist University, for his contributions to vertebrate paleontology.

Diagnosis.—Distal end (21.7 mm) of left tibiotarsus similar to that of *Neophrontops americanus* L. Miller (see Miller, 1916, and Howard, 1932, for generic diagnosis), but differing as follows: anterior intercondylar fossa relatively deeper; tendinal groove relatively broader; internal ligmental prominence relatively more pronounced; external ligamental prominence relatively less pronounced; shaft relatively more robust at condylar area; external condyle notched at its union with shaft (running smoothly into shaft in *N. americanus*). *N. slaughteri* is similar in size to the largest of the tibiotarsi of *N. americanus*, measured as follows: breadth of distal end of tibiotarsus—15.0 mm in *N. slaughteri* and 14.3 ± 0.8 (standard deviation) (range 13.2 to 15.0) in 6 *N. americanus*; depth of distal end of tibiotarsus—11.4 in *N. slaughteri* and 11.0 ± 0.5 (range 10.2 to 11.3) in 6 *N. americanus*.

DISCUSSION

With the description of *N. slaughteri*, there are now five species of the genus *Neophrontops* known from the fossil record of the New World. The oldest form, *N. vetustus* (Wetmore, 1943), was described on the basis of a humerus from the Miocene of Nebraska. It represents a species smaller than *N. americanus* and therefore presumably smaller than *N. slaughteri*. *N. dakotensis* was described on the basis of a humerus from the lower Pliocene of South Dakota (Compton, 1935). A coracoid from the middle Pliocene of Oregon has also been assigned to this species, on the basis of similar relative size and of general similarity of horizon (see Brodkorb, 1961). *N. dakotensis*, like *N. vetustus*, was a smaller form than *N. americanus* and *N. slaughteri*. The only other species, *N. vallecitoensis* (Howard, 1963), was described from the middle Pleistocene (Vallecito Creek fauna of the upper part of the Palm Spring Formation) of California, on the basis of a fragmentary tarsometatarsus that is somewhat larger than the same elements of *N. americanus*.

Neophrontops slaughteri would probably most closely approximate *N. vallecitoensis* in size, although it also overlaps the upper limits of *N. americanus*. *N. slaughteri* differs in important characters from *N. americanus*, and it occurred at a much earlier time than that species. The Vallecito Creek fauna (*N. vallecitoensis*) is older than that of Rancho La Brea (*N. americanus*), but younger than the Hagerman or Rexroad local fauna. Consequently, the Hagerman species, *N. slaughteri*, is at least a million years older than either of those two species. Although similar elements of all the forms

of *Neophrontops* are not available for comparison, it would appear almost certain from indirect evidence that *N. slaughteri* represents a distinctive species, albeit closely allied to the other North American species of the genus.

Because Old World vultures occur as early as the lower Miocene in both the Old and New Worlds (*Palaeohierax* and *Palaeoborus*, respectively), we have no firm evidence as to the group's area of origin. Additional fossils from earlier horizons will be needed to aid in answering this and other questions about the evolution of aegyptiines. *Neophrontops americanus* is osteologically close to the living Egyptian Vulture (*Neophron percnopterus*), an aegyptiine of Eurasia and Africa. The fact that *Neophron* is unknown from the Old World fossil record strongly suggests that the genus is derived from an invasion of the Old World by New World *Neophrontops* stock, possibly as late as Pleistocene time.

ACKNOWLEDGMENTS

The late Professor Claude W. Hibbard placed the specimen at my disposal and encouraged this study. I wish to thank the Los Angeles County Museum for the loan of specimens of *Neophrontops americanus*, and Dr. Robert W. Storer of the University of Michigan Museum of Zoology for the loan of specimens of *Necrosyrtes monachus* and *Neophron percnopterus*. I am indebted to Dr. Pierce Brodkorb for examining the fossil, and to Carolyn Moseley for her independent evaluation of the fossil. R. H. Wiley, H. C. Mueller, and Carolyn Moseley offered helpful suggestions on the manuscript. Mrs. Yvonne Lee skillfully rendered the camera lucida drawings for Fig. 1.

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27514. ACCEPTED 2 APRIL 1974.

NEW LIFE MEMBER



Daniel D. Berger is now a Life Member of The Wilson Ornithological Society. Mr. Berger belongs to many scientific societies and is an investor by profession. His interests in birds center on raptors, and he has authored or co-authored almost fifty publications. His works on raptor migration and Peregrine Falcons are especially notable. He is single and lives in Milwaukee, Wisconsin.

THE EFFECTS OF SUPERIMPOSED MAGNETIC FIELDS ON GULL ORIENTATION

WILLIAM E. SOUTHERN

In previous studies on orientation in the Ring-billed Gull (*Larus delawarensis*), I (Southern, 1967, 1969, 1971, 1972a, 1972b) have shown that: 1, chicks and juveniles give oriented directional responses when tested in orientation cages; 2, their preferred bearing corresponds to the mean angle between the nesting and wintering grounds as indicated by band recovery data; and, 3, geomagnetic cues may be associated with their ability to select a preferred heading under test conditions. During the summers of 1971 through 1973, I undertook additional studies on the effects of geomagnetism on orientation in chicks of this species. Recent publications by Keeton (1971), Merkel (1971), Wiltshcko (1968), and Wiltshcko and his colleagues (1971, 1972), dealing with pigeons (*Columba livia*) and European Robins (*Erithacus rubecula*), provide support for conclusions from my studies and those of Yeagley (1947, 1951) and Merkel and Wiltshcko (1965). However, despite these findings it is impossible to state unequivocally that any avian species orients by geomagnetic cues.

Almost every investigator in this field has his own apparatus design, uses different species, and often prefers different statistical procedures. As a consequence, direct comparison of results is extremely difficult if not impossible. The directional tendencies reported in some studies, particularly those relying on grouped responses for a small number of subjects (i.e., second order means) to designate 'preferred bearings,' may be statistically significant, but their biological significance is subject to question. Further work on this subject is essential, as the data supporting a hypothesis of migrational orientation by geomagnetic cues are not as convincing as those for the use of some other more readily accepted cue systems, e.g., stars.

This study was designed to provide a more accurate measure of the response of Ring-billed Gull chicks to alterations in the earth's magnetic field. In the first place, I am assuming that gull chicks do have a sense of orientation and that such orientation is a net direction toward the first migrational movement they will experience, i.e., south-southeast. My reasons for these assumptions are based on: 1, band encounter analysis for juveniles from the population studied; 2, results from experiments with free-flying juveniles; and 3, data from replication trials with chicks. The rationale behind this experimental approach has been discussed in a separate paper (Southern, in press). Experiments were designed to collect data for answering three basic questions: 1, will a magnetic field, when superimposed upon the geomagnetic field,

cause gull chicks to become disoriented?; 2, will a significant reduction in the earth's magnetic field result in disorientation?; 3, are gull chicks able to obtain directional information from artificially produced magnetic fields having various characteristics, particularly ones resembling the earth's components? Naturally occurring magnetic disturbances (i.e., geomagnetic storms) and sky conditions were also considered during field experiments.

METHODS

Ring-billed Gull chicks ranging in age between 3 and 10 days were obtained from the Calcite colony at the Michigan Limestone Division of the U.S. Steel Corporation near Rogers City, Presque Isle County, Michigan. The birds were transported by automobile to the research area located about 0.3 km from the colony. The age of each chick (in days) was recorded at the onset of the experiment and data for each age class were analyzed separately and also by three-day groupings, i.e., 3-6 days. This analysis indicated that chicks ranging between 3 and 10 days old responded similarly in the experimental apparatus. As a result, I am assuming that differences in age had no effect on orientation ability and the data have been combined for discussion in this paper.

Birds from this colony were selected because their migratory behavior had been studied more thoroughly than that of any other gull population of the Great Lakes Region (Southern, 1974). Analysis of encounter data for about 25,000 banded or wing-marked gulls has shown the mean direction travelled during fall migration to be approximately 165°. This bearing was used as the hypothesized preferred heading during statistical analysis of my orientation data. Headings taken by experimental gull chicks were tested to determine if they were consistent with the actual migratory behavior recorded for individuals from this population. Chicks from this colony also were used in my earlier experiments (1967, 1969, 1972a), so their adaptability to the experimental procedure had been documented. Because of the mainland location of this colony, it was possible to place test equipment far enough from adult gulls to avoid possible auditory contact between them and chicks used in trials.

Each year experiments were conducted throughout June and occasionally into early July. During the three summers my assistants and I conducted approximately 4,700 orientation-cage trials in addition to a group of free-flight trials (Southern, 1972b). Results directly applicable to the three basic questions posed above will be presented at this time. Data from the remaining trials have been omitted from this paper because similar material has been published earlier (Southern 1969, 1971, 1972a). Field trials were conducted by several observers, various assistants, and myself over the three-year period thereby verifying that the results are repeatable and not simply the interpretation of one person.

Each gull chick (3 to 10 days old) was used in only one orientation-cage trial. Therefore, the mean headings used in the text are based on this single choice-reaction by the number of birds tested under those particular conditions. This approach increased the likelihood that the calculated preferred headings were representative of the population studied rather than simply preferences of individual birds that were expressed repeatedly during additional trials.

Orientation-cage Design and Test Procedure.—The Southern-type orientation-cage was used for all trials. The standard cage was circular with 2-foot-high (0.6 m) opaque sides

of nonmagnetic materials. The top was open, thereby permitting experimental birds an unobstructed view of the natural sky during trials. It was set up on flat terrain with 360° corresponding to magnetic north. The ground formed the bottom for outdoor cages, but a wooden floor to which coarse sand had been glued was fastened to the elevated indoor models. The supporting upper and lower aluminum rings were marked off in 15° sectors, allowing an observer watching through one of the two portals in the side to plot the bird's course during a trial and its position at the termination of the experiment. The observer periodically switched from one portal to the other between groups of trials to reduce the likelihood that his location biased results. Two cage sizes were used, the diameters of outdoor and indoor models being 8 feet (2.4 m) and 5 feet (1.5 m), respectively. Trials were conducted simultaneously in the adjacent control and experimental chambers thereby assuring that both groups were subjected to the same uncontrolled variables.

Located in the cage center was a 10-inch-diameter (2.5 dm) holding chamber under which one chick was placed at the onset of a trial. This structure was raised above the arena side by means of a string and pulley arrangement attached to an overhead support, thereby providing the bird with an unimpeded choice of headings. Two people were required to operate each test cage. One functioned as the observer, recording existing environmental parameters and each bird's response during a trial on a printed replica of the cage floor. The other placed chicks in the test apparatus and removed them following trials.

A trial consisted of placing a gull chick under the holding chamber, freeing the bird by raising the chamber, and giving it two minutes to select and follow a course toward the cage wall. Trials were terminated when a bird reached the arena wall or when the allotted two-minute period had elapsed. The observer plotted the chick's course on a printed replica of the cage floor pattern. Final headings, the points at which birds reached the wall or their bearing after two minutes, were plotted to the nearest 5°. Final headings were used as indicators of directional preference. Occasionally chicks failed to respond and simply stood in the cage center and looked about. These were recorded as no responses and excluded from calculations. Chicks used in trials were selected at random from those available in the colony. Afterwards each was banded with a Fish and Wildlife Service band, which prevented us from selecting the same individuals for later experiments.

Initial headings, or the direction a chick faced at the onset of a trial, were also tested for significance. As none of these data showed a preferred bearing, I have concluded that the chicks do not elicit an oriented response until after the holding chamber has been raised. Therefore, the associated data have been omitted from this paper.

Production of Superimposed Magnetic Fields.—Three methods were used to alter the geomagnetic field in the immediate vicinity of gull chicks during orientation trials. Each method involved the use of magnets.

Small ceramic disc magnets (12-mm-diameter) were glued to the top of a gull chick's head or to the middle of its back with F-Bar-F Branding Cement (Victor Business Forms Co., 2105 Y St., Lincoln, Nebraska). The magnets produced a 0.5 Oersted field about the head. The direction of the field was perpendicular to the plane of the disc magnet. The polarity of the magnetic field, i.e., whether upward or downward, in relation to the bird's body was determined randomly by the person attaching the magnet. As a result, the differential effect of polarity was not considered during these particular trials although I now realize that it should have been. The two locations on the bird's body were used as an attempt to determine if a superimposed field close to the brain had a differ-

ent effect than when placed centrally on the body. Brass discs of about the same size and weight were glued to similar locations on controls.

In one set of experiments rows of bar magnets were aligned along radii on the cage floor. This resulted in an irregular field, i.e., of a scalloped design, within the orientation cage. The maximum total field intensity over the cage floor was increased to about 1.5 Oersted. The control cage lacked magnets and the gulls were exposed to an undistorted geomagnetic field during simultaneous trials.

During 1973, a pair of bar magnets was crossed and placed beneath five nests during the incubation stage. The 11 chicks that hatched in these nests were used in trials when three-days-old. This procedure resulted in their being subjected to a superimposed magnetic field (range 1 to 2 Oersted) during about two weeks of development. These birds were exposed to the normal geomagnetic field during trials as were controls. The controls, however, were taken from nests not having superimposed fields during any stage of development.

During all of these trials, consideration was given to the effect of naturally occurring magnetic disturbances. Trials conducted during low, moderate, or severe conditions, indicated by K-indices provided by the World Data Center, were analyzed separately. All of the data presented in this paper pertain to low level disturbances.

Magnetically-shielded Room (MSR).—The MSR, with interior dimensions of 8×8 ft (2.5×2.5 m) on the floor and 6 ft (1.8 m) in height, was constructed by nailing and gluing 0.25-inch (6 mm) marine plywood over both sides of a framework of 2×2 inch (2.5×2.5 cm) struts. The interior walls were covered with 0.031 inch (0.8 mm) thick, Co-Netic magnetic shielding alloy (Perfection Mica Co., Bensonville, Ill.). This material had been hydrogen annealed to provide minimum degradation in magnetic shielding properties due to cold working. All joints were covered with seam strips held down with aluminum channel screwed to the wooden frame. This procedure provided magnetic shielding continuity between adjacent sheets. All fasteners were of nonmagnetic material (either aluminum or brass). The structure could be dismantled into six pieces for transport to a new test location.

An 8-inch (2 dm) hole was cut in the center of the ceiling and a 10-inch (2.5 dm) stack was constructed from shielding material to vent combustion gasses from propane lanterns used for interior lighting. A 2.5 foot (0.75 m) door was cut in one side. Overlapping strips of shielding around the door maintained magnetic continuity when the door was closed.

The MSR disturbed the ambient magnetic field for a distance of about 100 feet in any direction. Measurements were taken with a RFL Model 101 magnetometer to obtain a maximum field reading in space and a maximum field reading in the horizontal plane. The total maximum field outside the influence of the MSR was 60,000 gamma ($60k \Gamma = 0.6$ Oersted). The horizontal component was in the range of 13 to 14k Γ . All of the other test and control apparatuses were placed at locations far enough from the MSR to insure normal ambient readings.

Interior field measurements were made at two-foot intervals throughout the volume of the MSR. The mean magnetic field was 2317 Γ . If the ambient external field was taken as 60k Γ , then the mean attenuation factor is 0.04, and the ambient field was reduced by a factor of 25. In the 15 cm horizontal plane (centered on a point halfway between the floor and ceiling) the field variation was 24 percent and the gradient was 6.4 Γ/cm . The 5-foot-diameter orientation-cage used in the MSR was placed on legs so that the floor was within this level of field uniformity.

A control room of similar dimensions but without magnetic shielding was located

about 150 feet from the MSR. The test cage in this structure was similarly positioned on legs.

Lighting in each chamber was by two propane lamps (about 300 watts/lamp). The light provided was below optimum levels but a better source was not available, because the use of AC power sources involved further shielding and design problems that could not be resolved under current budget limitations. Because of this, chicks were tested at light intensities far below that outside the chambers.

Simulation of Geomagnetic Field Conditions.—The coil configurations for the MSR are based on modifications of a Rubens' coil set that consisted of five separate coils, each wound around the four of the six sides of a cube (see Rubens, 1945). Using Rubens' technique, equations were derived to determine the magnetic field due to a rectangular coil anywhere in space. As several coils are used, each wound around the z-axis, one may adjust the number of turns in each set of two coils symmetrical about the x-y plane (i.e., the plane of the central coil) to obtain maximum magnetic field homogeneity along the z-axis. The magnetic field at a given point within the Rubens' set is the vector sum of the fields due to each individual coil. Computer simulation indicated that the horizontal component of the desired field could be produced with a 5 coil Rubens' set whose turns ratio was 37:12:20:12:37. This set, wound over a 6×8 foot (1.8×2.5 m) rectangle with individual coils spaced two feet (0.6 m) apart, produced a field in the MSR's horizontal median plane (3 feet off the floor) that varied by no more than 11 percent in the 5-foot-diameter (1.5 m) test cage.

As gulls in the orientation cage were confined more or less to a horizontal plane, the demand for field homogeneity in the vertical direction was less stringent. The vertical field component was produced with a 3 coil Rubens' set, having a turns ratio of 23:10:23, wound over an 8×8 foot (2.5×2.5 m) square, with individual coils 3 feet (0.9 m) apart. Maximum field variation in the median horizontal plane was 7.3 percent for the 5-foot-diameter cage. When simulating the earth's magnetic field, both in magnitude and direction with the two coil sets, the maximum combined variation for a five foot diameter cage was 7.8 percent. Each coil was mounted in a frame of aluminum channel which was screwed to the channel covering the seam strips in the MSR. In addition to serving as support and protection for the coil windings, the channel also provided additional cooling area for the coils when operated with large currents.

Current was provided by two 12-volt heavy duty car batteries connected either in series or parallel, depending upon the range of field magnitude desired. It was possible to produce horizontal fields ranging between zero and 0.374 Oersted and vertical fields ranging between zero and 1.410 Oersted. Inclination of the field is changed from zero to 90° by adjusting the magnitude of the two field components. The batteries and controls (potential dividers, etc.) were located outside of the MSR.

Two fluxgate magnetometer probes were mounted just under the orientation cage floor, one oriented along the vertical coil axis and the other parallel to the horizontal coil axis. Leads from the probes were connected to a magnetometer located near the control box. Field settings were checked and adjusted several times during operation to offset voltage decrease due to battery discharge and/or resistance increase due to coil heating.

Statistical Treatment of Data.—Final headings and the parameters pertaining to each trial were punched on computer cards for analysis by an IBM 360/67. The mean angle, standard angular deviation, and the Rayleigh test (Batschelet, 1965; Zar, 1974) were calculated by means of a program prepared by Dr. J. H. Zar. Calculation of the probability of Rayleigh's statistic z and the modified Rayleigh test (V-test of circular uniformity) (Batschelet, 1972; Zar, 1974) were performed on a Hewlett-Packard Model

9100B programmable calculator. The null hypothesis of the standard Rayleigh test states that the theoretical distribution is uniform. When the test statistic z (tabular presentation of vector length) exceeds a certain critical value, the null hypothesis is rejected. The V -test is used when a particular direction is expected to be the preferred direction in advance of the experiment. In the case of Ring-billed Gulls from Rogers City, Michigan, the preferred heading of 165° , corresponding to the direction of fall migration, is already known in advance. The null hypothesis to be tested is randomness, meaning that the angles of the sample are independent observations from a uniform distribution. Use of the V -test is preferable when knowledge of a predicted direction is available, as it provides a more powerful test. The V -test leads to significance only if there is a sufficient clustering around the predicted direction. In contrast, the Rayleigh test is less powerful in this case but remains powerful for clustering on any part of the circle (Batschelet, 1972).

RESULTS

Standard-cage Controls

Inconsistencies exist in the control data for specific years. In some cases clear sky trials showed significant mean headings, whereas the overcast trials did not. Occasionally the reverse is true. In other instances the mean heading represents a significant sample mean rather than a significant population mean. The presence of conflicting results for the controls has made it even more difficult to evaluate the data for experimental groups. No explanation for the inconsistencies is available at this time.

TABLE I
STATISTICS FOR STANDARD CAGE CONTROL TRIALS, 1971-1973

| | N | Mean angle | Angular deviation | Rayleigh z | Prob. z | V-test 165° | Signif. level | Number of no responses (percent) |
|-----------|-----|------------|-------------------|--------------|-----------|--------------------|---------------|----------------------------------|
| 1971-73 | | | | | | | | |
| Clear sky | 357 | 162.59 | 74.95 | 7.45 | .0005 | 51.52 | .0005 | 46 (11) |
| Overcast | 312 | 169.41 | 78.43 | 1.24 | .2885 | 19.64 | not (.10) | 44 (12) |
| 1971 | | | | | | | | |
| Clear sky | 94 | 191.86 | 74.19 | 5.07 | .0062 | 27.97 | .0005 | 9 (9) |
| Overcast | 96 | 225.80 | 75.98 | 2.27 | .1032 | 9.18 | not (.10) | 10 (9) |
| 1972 | | | | | | | | |
| Clear sky | 180 | 190.16 | 72.03 | 12.06 | .00001 | 52.05 | .0005 | 20 (10) |
| Overcast | 133 | 89.30 | 78.51 | 0.90 | .4067 | 3.36 | not | 17 (11) |
| 1973 | | | | | | | | |
| Clear sky | 83 | 73.90 | 66.79 | 8.53 | .0001 | - 0.51 | not | 17 (17) |
| Overcast | 83 | 131.80 | 72.47 | 3.32 | .0355 | 13.90 | .025 | 17 (17) |

In Table 1, test statistics for each of the three years have been presented separately for clear and overcast sky conditions. In addition, the grouped data for the three years have been plotted according to sky condition. All 669 trials were conducted during low intensity disturbances in the geomagnetic field (K -indices 0-3). The clear sky results for 1971, 1972, and 1971-73 (combined) were significant according to the Rayleigh and V -tests. The mean angles ranged between 163 and 192° for these three sets of data. In contrast, the overcast headings were not significant. The reverse was true for 1973, except that the clear sky heading was significant by the Rayleigh test but not so according to the V -test. This means that a significant sample mean existed in the 1973 data, but that the birds failed to show a preference for the hypothesized population mean. The fact that the 1973 controls exhibited a significant direction preference (132°) during overcast conditions makes it appear unlikely that the discrepancies for the other years are the result of chicks using solar cues.

The relative frequency of final headings under clear and overcast skies are

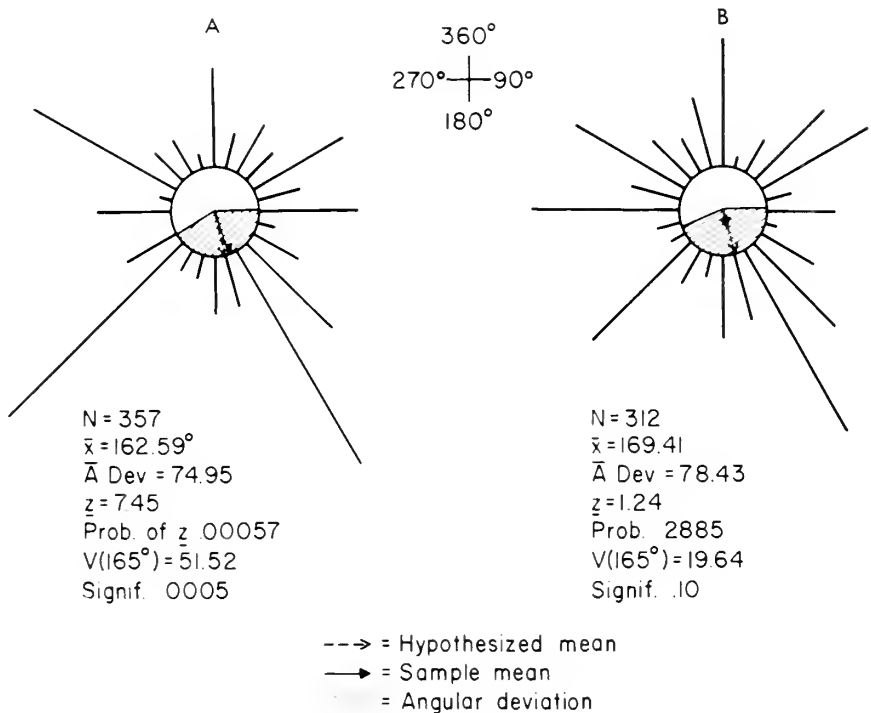


FIG. 1. A. Relative frequency of responses for chicks tested as controls in standard-cage under clear skies, 1971-73. B. Similar data for chicks tested under overcast skies.

present for the combined years (1971-73) in Figure 1. The mean angle for overcast trials is similar to that for clear trials, but it is significant at only the 90 percent level. Although the distribution of these final headings is approaching randomness, the overall pattern is still very different from that for trials involving superimposed magnetic fields. Similar discrepancies had not been present in clear versus overcast data from previous years of inquiry (Southern, 1969, 1972a). An explanation for the change is not apparent at this time. I do not interpret it as an indication that sun cues are being used by chicks, because there is no consistent response pattern in relation to the availability of solar cues.

TABLE 2
STATISTICS FOR STANDARD CAGE EXPERIMENTALS—SUPERIMPOSED FIELDS

| | N | Mean angle | Angular deviation | Rayleigh z | Prob. z | V-test 165° | Signif. level | Number of no responses (percent) |
|---------------|-----|------------|-------------------|--------------|-----------|-------------|---------------|----------------------------------|
| 1971-73 | | | | | | | | |
| Clear sky | 388 | 29.88 | 78.19 | 1.83 | .1598 | -18.90 | not | 71 (15) |
| Overcast | 327 | 331.68 | 79.79 | 0.30 | .7413 | - 9.63 | not | 43 (12) |
| 1971 | | | | | | | | |
| Clear sky | 118 | 58.95 | 80.57 | 0.01 | .9899 | - 0.25 | not | 21 (15) |
| Overcast | 91 | 293.92 | 76.86 | 0.91 | .4020 | - 5.73 | not | 19 (17) |
| 1972 | | | | | | | | |
| Clear sky | 180 | 110.22 | 76.06 | 0.34 | .7130 | 5.81 | not | 30 (14) |
| Overcast | 148 | 292.27 | 72.32 | 0.45 | .6390 | - 6.41 | not | 12 (8) |
| 1973 | | | | | | | | |
| Clear sky | 90 | 8.22 | 67.85 | 8.03 | .0002 | -24.71 | not | 20 (18) |
| Overcast | 88 | 51.40 | 77.16 | 0.72 | .4873 | - 3.10 | not | 12 (12) |
| BODY MAGNETS | | | | | | | | |
| 1971 | | | | | | | | |
| Clear sky | 137 | 13.76 | 79.58 | 0.17 | .8416 | - 4.27 | not | 13 (9) |
| Overcast | 79 | 182.27 | 78.38 | 0.33 | .7224 | 4.85 | not (.25) | 21 (21) |
| FLOOR MAGNETS | | | | | | | | |
| 1971 | | | | | | | | |
| Clear sky | 97 | 74.10 | 79.64 | 0.11 | .8939 | - 0.05 | not | 13 (12) |
| Overcast | 85 | 228.81 | 68.26 | 7.16 | .0007 | 10.89 | .05 | 15 (15) |
| NEST MAGNETS | | | | | | | | |
| 1973 | | | | | | | | |
| Clear sky | 11 | 324.97 | 68.96 | 0.84 | .4433 | 2.85 | not (.25) | 0 (0) |

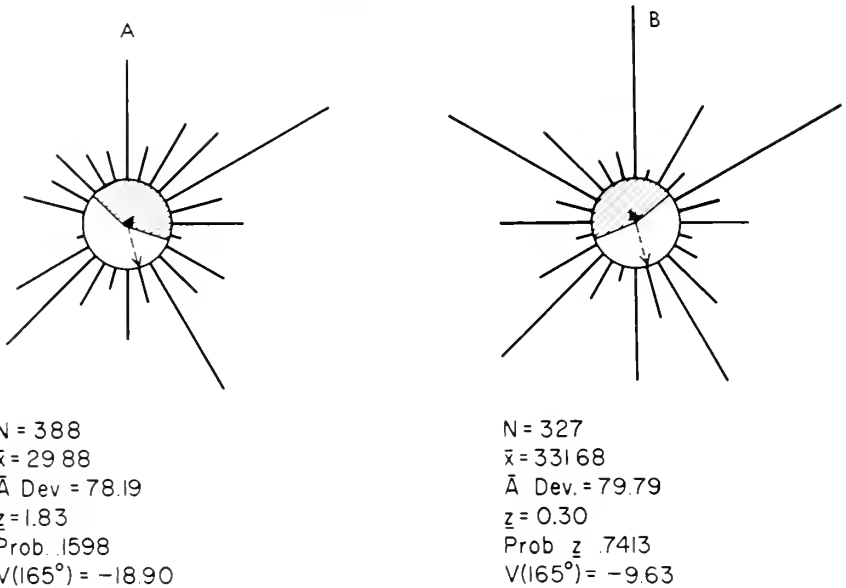


FIG. 2. A. Relative frequency of responses for chicks tested under clear skies in a standard-cage while wearing head magnets, 1971-73. B. Similar data for trials conducted under overcast conditions.

Superimposed Magnetic Fields

During all three years, trials were conducted with experimental gulls bearing head magnets. In all, 715 trials were conducted under clear and overcast skies. In no instance did birds wearing head magnets show (Table 2) a significant preference for the hypothesized population mean (165°). A significant sample mean (3.22) occurred in the data for 90 trials conducted under clear skies in 1973. The relative frequencies of headings for the 1971-73 clear and overcast head magnet trials are plotted in Figure 2. The results for experimental chicks and those for standard controls (Table 1) are obviously different. The almost complete loss of an ability to select a preferred heading indicate that a superimposed magnetic field will disrupt the orientational ability of young Ring-billed Gulls.

Body magnets and nest magnets also resulted in disorientation. In the case of the former, final headings were randomly arranged during clear as well as overcast conditions. Results for nest magnet trials are particularly interesting because in this case chicks were not subjected to a superimposed field during the actual trial. Instead, an experimental field had been applied during embryological development. These results suggest that the magnetic field sur-

TABLE 3
STATISTICS FOR TRIALS IN THE MAGNETICALLY-SHIELDED ROOM (MSR) AND
CONTROL CHAMBER

| | N | Mean angle | Angular deviation | Rayleigh z | Prob. z | V-test 165° | Signif. level | Number of no responses (percent) |
|-------------------|-----|---------------|----------------------|-----------------|--------------|----------------|------------------|--|
| MSR | | | | | | | | |
| 1971-73 | 101 | 240.19 | 77.20 | 0.86 | .4240 | 2.38 | not | 497 (83) |
| 1971 | 26 | 247.44 | 59.30 | 5.61 | .0029 | 1.59 | not | 173 (87) |
| 1972 | 43 | 189.46 | 76.93 | 0.42 | .6614 | 3.86 | not (.25) | 157 (79) |
| 1973 | 32 | 41.98 | 73.57 | 0.99 | .3757 | 3.06 | not | 167 (84) |
| Controls | | | | | | | | |
| 1971-73 | 122 | 96.02 | 72.99 | 4.34 | .0128 | 8.25 | not (.25) | 179 (60) |
| 1971 | 69 | 111.07 | 76.37 | 0.86 | .4249 | 35.13 | .0005 | 31 (31) |
| 1972 | 32 | 79.72 | 65.85 | 3.69 | .0237 | 0.89 | not | 69 (68) |
| 1973 | 21 | 107.58 | 70.19 | 1.31 | .2731 | 2.82 | not (.25) | 79 (79) |
| 1973 ¹ | 90 | 197.38 | 78.36 | 0.31 | .7368 | 4.44 | not | 10 (10) |

¹ With translucent roof.

rounding a prehatched Ring-billed Gull influences, in some way, its later ability to use ambient geomagnetic cues for orientation purposes.

Results for floor magnet trials were not as conclusive. The clear sky trials ($N = 97$) lacked a significant heading, whereas trials conducted under overcast conditions ($N = 85$) had a significant bearing (0.05). Although I am unable to account for this difference, the fact that gulls tested during overcast showed a significant preference for 165° makes it seem unlikely that they were responding to solar cues; therefore, some other factor must be responsible.

Effect of Reduced and Simulated Fields

MSR and Control Room.—The data for this group of trials are presented in Tables 3 and 4. The response rate was poor for trials conducted in the two buildings. I believe that low light intensity in the MSR and control building contributed to the large number of no responses (79-87 percent in the MSR; 31-79 percent in the Control Room). It is also possible that the reduced magnetic field, in the MSR affected the tendency for gull chicks to respond. Support for this possibility is provided by the finding of El'Darov and Kholodov (1964), that the rate of particular motor activities of various passerines is increased as magnetic field intensity is increased to about three times that of the earth. It is possible that reduced field intensity has the opposite effect.

During the three years of MSR trials with reduced field intensity, no

TABLE 4
STATISTICS FOR TRIALS CONDUCTED WITH SIMULATED MAGNETIC FIELDS

| | N | Mean angle | Angular deviation | Rayleigh z | Prob. z | V-test 165° | Signif. level | Number of no responses (percent) |
|---------------------|----|------------|-------------------|--------------|-----------|-------------|---------------|----------------------------------|
| MSR-4A ¹ | 21 | 163.49 | 62.62 | 3.41 | .0312 | 8.45 | not (.25) | 29 (58) |
| MSR-4B ² | 4 | 214.38 | 65.27 | 0.49 | .6406 | 0.91 | not | 16 (80) |
| MSR-4C ³ | 14 | 122.25 | 70.64 | 0.81 | .4545 | 2.47 | not (.25) | 21 (60) |
| MSR-4D ⁴ | 14 | 185.48 | 74.49 | 0.34 | .7218 | 2.03 | not (.25) | 26 (65) |

¹ Field equivalent to earth's, 0.6 Oersted.

² Field twice that of earth, 1.2 Oersted.

³ Field one-half that of earth, 0.3 Oersted.

⁴ Experimental north shifted 180° from ambient north.

significant preference was indicated by chicks for the predicted heading of 165°. However, the 26 birds that responded in 1971 had a statistically significant mean bearing of 247°. The combined responses for the three years lack a preferred bearing (Fig. 3B).

Response rates in the control chamber were lower than in outdoor trials, but not as low as in the MSR (Table 3). Although the combined results for the three years did not indicate a significant preference for 165°, there was a significant sample mean of 96° (Fig. 3A). In addition, the results for 1971 and 1972 were significant by one statistical test or the other. As with the superimposed field trials, the results are more consistent. In the latter instance, it appears that an alteration in the normal geomagnetic field causes an overall response pattern different from that for controls. There seems to be a trend in each data set suggesting that disturbances in the earth's magnetic field will disrupt the ability of Ring-billed Gull chicks to select a preferred bearing. In addition, it appears that a reduction in the opportunity for chicks to see other aspects of their natural environment, e.g., the landscape or sun, may reduce the extent to which their orientation ability is expressed during experimentation.

Various attempts were made to determine if low light levels were associated with the reduced response rates. One method for testing this was to replace the opaque roof (plywood) of the control room with sheets of translucent fiberglass. By doing so, the number of no responses was decreased from 56 percent for the combined years of 1971-73, to 10 percent for 1973 (Table 3). Similar changes could not be made in the MSR ceiling without destroying the shielding effect. The differences in response rates indicate that an improved lighting method for both rooms might have increased the response rate of chicks, as well as the validity of this important group of trials.

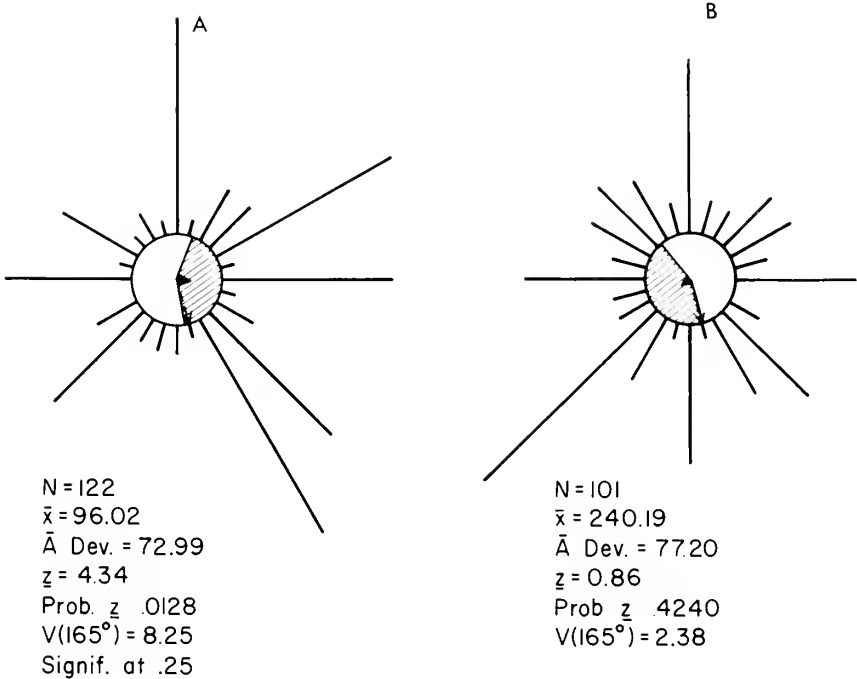


FIG. 3. A. Relative frequency of responses for chicks responding in the unshielded control room during 1971-73. B. Similar data for birds tested in the magnetically-shielded room (MSR).

While it appears that reductions in the total intensity of the geomagnetic field (by a factor of 25) has some effect upon the orientation ability of Ring-billed Gull chicks, data from these experiments are not sufficient for proving such a contention.

Simulated Fields.—Four different magnetic field conditions were produced by the coil system in the MSR. Fifty trials were conducted under the influence of an artificial field having a total intensity equal to that of the Rogers City area (0.6 Oersted). Only 21 (62 percent) of the chicks responded (see MSR-4A in Table 4). The resulting mean angle (163°) represented a significant sample mean, but not a significant predicted mean except at the 0.25 level. These results suggest that Ring-billed Gull chicks may be capable of obtaining directional information from a simulated field having component characteristics similar to those of the geomagnetic field.

Three other artificial magnetic field conditions were used (Table 4), none of which resulted in significant mean headings by chicks. Only four (20 per-

cent) out of 20 chicks responded during tests under the influence of an artificial field having a total intensity about twice (1.2 Oersted) that of the earth (see MSR-4B in Table 4). In another set of trials, 14 (40 percent) of the 35 chicks exposed to a field of one-half (0.3 Oersted) that of the earth at Rogers City responded during trials (see MSR-4C in Table 4). The sample sizes for responding birds were small in both instances, but it appears that gull chicks lack a directional preference when suddenly subjected to fields either significantly higher or lower than the one experienced during development or immediately before the trial. In 1973, 25 chicks were held in the MSR for 15 to 60 minutes before trials: such exposure did not improve response rates.

I also subjected 40 gull chicks to a field of about equal intensity to the earth's, but having experimental north rotated 180° from geomagnetic north (see MSR-4D in Table 4). Only 14 (35 percent) of the chicks responded, and these showed an almost random pattern of headings (significant at 0.25 level). In general, the results from the trials with simulated fields must be considered inconclusive. The low response rate discouraged me from conducting additional trials, as I consider it inappropriate to base any final decisions about orientational ability on the response of such a small proportion of the available population.

DISCUSSION

From the data presented in this paper, it is impossible to state conclusively whether or not Ring-billed Gulls are using geomagnetic cues for orientation. Part of the difficulty associated with interpretation of results from such studies may rest with our basic methodology.

During orientation experiments we have no assurance that a majority of our test subjects are in the proper endogenous state to do what we expect at a particular moment. We also lack an awareness of the complex of stimuli in existence at any moment or what the priorities might be. Furthermore, the controlled elimination of particular variables may significantly reduce the likelihood of any response, while not having any direct effect on the behavior under study (i.e., orientation). We also are unaware of the effect an experimenter has on the probability that particular individuals will respond in a given way. From past experience with capturing and releasing adult Ring-billed Gulls in homing trials (1967), I know that extensive differences appear in the reaction to being 'manhandled.' Adults used as controls were released at the colony after being subjected to trapping, marking, and the other treatments applied to experimental birds. The response of these birds varied greatly, some immediately abandoned the colony, other stayed away from the nest area for hours, and a proportion returned immediately. In the litera-

ture such time intervals have been used to designate poor, average, and outstanding homing performance. Similar types of reactions to the rigors of the experiment should be expected from gull chicks, and probably from other species as well. This sort of information is not usually plugged into data analysis and for good reason, we do not know how to handle it, except that we try to treat controls similarly.

Perhaps we should be more willing to accept substantiated trends as being indicative of what a species can or cannot do. From this baseline, more precise questions can be asked and appropriate techniques developed to give answers regarding the minutia associated with the mechanisms responsible for the varied results. If our level of investigation is going to advance, it is necessary for researchers in the area of avian orientation, and their critics, to accept the existence of variability, to probe its basis, and to acknowledge that the general trends reported for various cue systems are adequate for advancing us to the next stage of inquiry. At this new level of investigation it should be possible to analyze the actual processes and the associated mechanisms.

This is the light in which my current results should be evaluated, and hopefully the preceding comments will serve as adequate justification for so doing. If we compare the results for the experimental groups exposed to superimposed magnetic fields with those for controls tested outdoors in the natural geomagnetic field, it is obvious that differences exist. Most of the test groups lack a preference for the predicted population mean of 165° . In addition, almost all of the experimental groups lacked a preferred mean heading. The trend in the experimental data is that of randomness.

On the other hand, the control groups often had a preferred heading corresponding to the predicted mean, or they indicated a tendency toward a preference for some direction, even though it is not always significant at levels above 95 percent. This strongly suggests that the gull chicks are sensing magnetic stimuli and that spontaneous, or unusual, alterations in the geomagnetic field (or the field they experienced during development) will reduce or cause an elimination of their tendency to exhibit a directional preference. It may be true that Ring-billed Gull chicks are actually deriving directional information from magnetic cues, but my attempts to verify this possibility were unsuccessful. I did not, however, obtain data that negate such a possibility. Further work is essential to explain the extent of such an avian ability and to locate the mechanisms involved.

SUMMARY

A three year study was undertaken to determine the role of geomagnetic cues in Ring-billed Gull orientation. The study was designed to provide data for answering three basic questions: 1, will superimposed magnetic fields cause disorientation?; 2, will reduc-

tions in the geomagnetic field result in disorientation?; 3. are gull chicks able to obtain directional information for artificial magnetic fields?

Orientation-cage experiments were conducted in the natural environment, in a magnetically-shielded room (MSR) equipped with Rubens' coils, and in an unshielded control room. Detailed descriptions of the equipment and test procedures are provided. The resulting data were tested for the presence of a significant sample mean and for the clustering of responses about a predicted population mean. The latter test took into account information based on the migratory history of gulls from the colony under study.

Certain inconsistencies exist in the data and an attempt has been made to account for some of these. In general it appears that any significant alteration in the geomagnetic field will cause Ring-billed Gull chicks to disperse randomly in the test apparatus. In contrast chicks tested as controls usually indicated a preferred heading. It appears that Ring-billed Gulls are capable of perceiving geomagnetic stimuli and that their ability to express a directional preference may be based on such cues.

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ENTRY AND EXIT OF SYRINGOPHILID MITES
(ACARINA: SYRINGOPHILIDAE) FROM THE LUMEN
OF THE QUILL

STANLEY D. CASTO

Several species of mites are known to inhabit the quills of bird feathers (Wehr, 1952; Radford, 1953; Kethley, 1970). Obviously entry and exit from the quill must be either through the superior umbilicus or through specially constructed openings, but no adequate descriptions exist of the methods utilized. Whether the superior umbilicus remains open, allowing free access, or closes during formation of the quill is not clarified in the literature. Although feather development has been extensively studied (Lillie, 1940; Lucas and Stettenheim, 1972), the "umbilical plug" which seals the superior umbilicus has not been well described.

The quill mite, *Syringophiloides minor* (Berlese) is a common parasite of the House Sparrow (*Passer domesticus*) and provides an excellent example of how mites have adapted to life within the quill. After the internal pulp has been resorbed, the mites feed by piercing the quill wall with their styletiform chelicerae (Kethley, 1971). Adult female mites emerge from mature quills and disperse to enter developing feathers. Transfer of mites from the feathers of parent birds to the developing feathers of nestlings presumably occurs during diurnal brooding or nest roosting. During molt the mites disperse from the old quills into the developing feathers of the new plumage (Kethley, 1971; Casto, 1973; 1974). In this report, I describe those aspects of feather development and structure which affect entry and exit of *S. minor* from the quill.

MATERIALS AND METHODS

From January 1971 through July 1972, 492 House Sparrows ranging in age from nestling to adult were collected in the vicinity of Lubbock, Texas. Examination for mites consisted of plucking the primaries, major primary coverts, secondaries, major secondary coverts, alulars, and rectrices, followed by opening the quill of each feather to determine infestation. Mites were recovered from the exsheathed feathers of nestlings and the developing feathers of molting birds by peeling away that portion of the sheath which lies proximal to the unfurled vanes.

As the external pulp of the primaries, secondaries, and rectrices is resorbed and the vanes exsheath, the superior umbilicus generally becomes closed by a structure which I have designated as the umbilical plug. The plug consists of the dried pulp membrane, the degenerating axial artery, and incompletely resorbed blood and mucus. The normal appearance of the plug is that of a tiny blood clot. Virtually all of the larger feathers have a plug, even though it may consist of only the dried, transparent pulp membrane. Observations on the formation of the umbilical plug and its role in regulating entry of

mites into the quill lumen were made from those developing feathers of nestlings, fledglings, and molting birds which were in the last stages of exsheathment and resorption of the external pulp.

The structure of the umbilical plug in mature quills was demonstrated from freehand sections. Sections were photographed and the negative projected with an enlarger. The outline was traced and compared with the original in order to draw in details.

Twenty molting House Sparrows were kept under laboratory observation for several weeks in an attempt to determine if mite infestations produce feather loss, feather picking, or irritable behavior. At the end of the observation period the birds were sacrificed and examined to determine the extent of infestation.

RESULTS AND DISCUSSION

Eighty-two percent (402) of the 492 House Sparrows examined were infested. The primaries, major primary coverts, secondaries, and rectrices were the most commonly infested feathers. An average of 13 feathers (range = 1 to 42) was infested per bird. The youngest bird infested was a nestling estimated by the degree of feather exsheathment (Weaver, 1942) to be 11 days old.

The mites exhibit a preference for different feathers and feather tracts in the juvenal and first nuptial plumages. These preferences appear to be due to certain developmental features of the juvenal feathers and the sequence with which the feathers of this plumage are replaced during the postjuvenal molt (Casto, MS).

Entry Into the Developing Feathers.—Female mites enter the superior umbilicus of developing feathers after the protective sheath has split from the pinfeather. That portion of the sheath immediately proximal to the unfurled vanes appears as an opaque white region (Lucas and Stettenheim, 1972) and serves to retard water loss from the pulp apex (Lillie, 1940). This portion of the sheath also serves to protect from exposure those mites which have entered the superior umbilicus of a developing feather.

Upon entry into the umbilicus of a developing feather, mites move proximally 2–5 mm until they reach the apex of the pulp. The anterior ends of the mites point proximally and lie near the pulp apex, suggesting that the pulp is the food source. As many as six mites have been recovered from a single feather.

Mites in developing feathers are found laterally appressed to the rachis at the point where the vanes are attached. In this position the mites lie between the two layers formed by the rachis with its attached vanes and the pulp membrane. As the external pulp is resorbed and the vanes exsheath the mites move proximally along the rachis, always maintaining their position between the two layers.

Occurrence of the Umbilical Plug.—Umbilical plugs are frequent features

TABLE 1
OCCURRENCE OF UMBILICAL PLUGS IN THE REPLACEMENT FEATHERS
OF MOLTING HOUSE SPARROWS

| Feather tract | Number examined | Plug present (percent) | Plug absent (percent) |
|---------------|-----------------|------------------------|-----------------------|
| Primaries | 269 | 221 (82) | 48 (18) |
| Secondaries | 227 | 202 (89) | 25 (11) |
| Rectrices | 184 | 153 (83) | 31 (17) |
| Total | 680 | 576 (85) | 104 (15) |

in the remiges and rectrices of the House Sparrow (Table 1) and also occur in the major primary coverts. Contrary to the observation of Kethley (1971), the umbilici of the primary coverts of adult sparrows do not always remain open allowing free access to the quill lumen. Of 216 juvenal primary coverts examined, 78 (36 percent) had plugs. Plugs in the primary coverts are not seated as firmly as those in the larger feathers.

Movement of Mites Through the Umbilicus.—Female mites enter the passageway of the superior umbilicus at the time of plug formation. The strand of material composing the plug in its early formation is soft and can be pushed to one side as the mite moves into the passageway. Movement through the passageway is hazardous, and mites often become ensnared in exudates of the degenerating pulp. When a hardened plug is removed from a mature feather and closely examined, it is often found to contain the remains of a mite. Occasionally two and sometimes three dead invaders are found in the umbilicus.

Structure of the Umbilical Plug.—The structure of an umbilical plug from primary number 5 is shown in Fig. 1. The passageway in which the plug is seated is a continuation of the ventral groove of the rachis. The cortical layer of the groove continues proximally as the dorsal lining of the umbilical passageway. The dorsal lining of the passageway becomes thinner as it nears the lumen of the quill.

The proximal end of the umbilical plug is continuous with the pulp membrane which forms the first internal pulp cap. The wedge shape of the hardened plug insures that mites attempting entry would only seat the plug more firmly into the umbilicus. Exit of mites from the lumen is by destruction of the fragile strand which connects the first internal pulp cap with the plug. The plug may then be displaced distally into the ventral groove.

Exit Channels.—If the plug cannot be displaced, the mites construct an exit channel by cutting through the thin cortex and soft medullary tissue (pith)

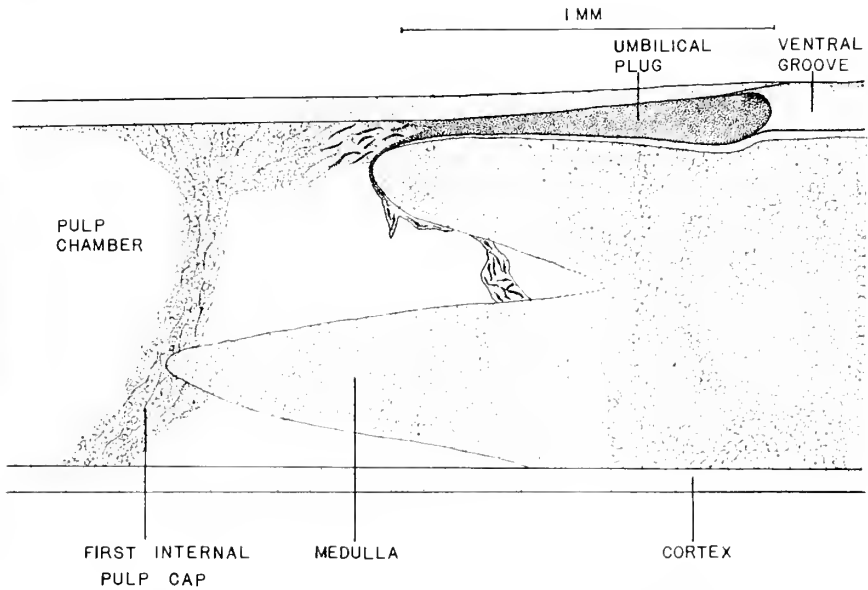


FIG. 1. Umbilical plug of primary number 5 (lateral section)

in the dorsal region of the passageway (Fig. 2). Construction of the exit channel is at an oblique angle to the ventral groove and leaves the plug intact. On several occasions two exit channels, one on each side of the plug, were observed. The means by which the mites produce the exit channel is not known. I have found no evidence that *S. minor* constructs any type of hole or channel for entry into the quill.

Kethley (1969) collected representatives of five genera of syringophilids from quills which had a small hole immediately distal to the superior umbilicus. When the infested quills were isolated in small tubes the mites were observed to leave the quills via these holes. I have also found these holes in the quills of Brown-headed Cowbirds (*Molothrus ater*) infested by syringophilids. These holes are probably produced by mites which move from the quill lumen into the cavity of the rachis and then burrow ventrally through the pith and cortical layer of the ventral groove.

The Effects of Infestation of Syringophilid Mites.—Several authors (Rebrassier and Martin, 1932; Schwage, 1956; Hwang, 1959) have noted the loss of plumage which occurs when domestic chickens are infested by *Syringophilus bipectinatus*. Critsenko (1973) believed that the feeding of *S. bipectinatus* produced an itching which caused chickens to pick at infested feathers. Feather loss was thought to result from a relaxation of muscle tonus.

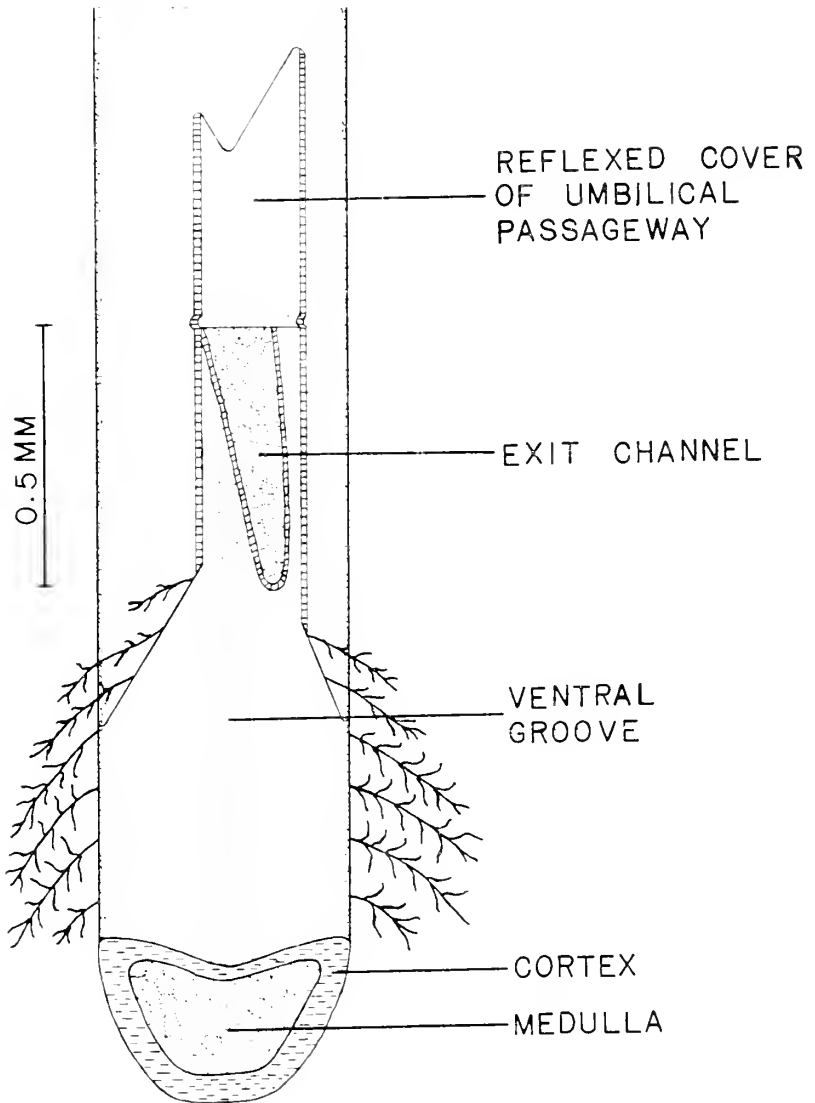


FIG. 2. Exit channel produced by the quill mite, *Syringophiloides minor*.

thereby allowing the developing feather germ to push the old, infested feather from its follicle. A decrease in productivity was also noted during infestation by *S. bipectinatus*. Wehr (1952) has reported feather loss and feather picking when developing feathers of the House Canary are infested by the dermoglyphid mite, *Dermoglyphus elongatus*.

I found no evidence of feather loss in House Sparrows infested by *S. minor*. The exit channels and the many small holes which are produced in the quill wall by the feeding activities of the mites do not appear to structurally weaken the feather. Although several of the sparrows kept under observation were infested, they did not pick at their feathers or show any indication that they were irritated by the mites.

SUMMARY

Eighty-two percent (402) of 492 House Sparrows collected in the vicinity of Lubbock, Texas, were infested by the quill mite, *Syringophiloides minor* (Berlese). An average of 13 feathers (range = 1-42) was infested per bird. The youngest bird infested was estimated to be 11 days old. Dispersing female mites enter the superior umbilicus of developing feathers. Entry into the lumen of the quill is regulated by formation of a plug which seals the superior umbilicus during feather development. Once seated in the umbilical passageway, the wedge-shaped plug prevents further entry of mites. Exit from the lumen of the quill is accomplished by displacement of the plug into the ventral groove or by specially constructed exit channels. The exit channels and the small holes which are produced in the quill wall by the feeding activities of the mites do not appear to structurally weaken the feather.

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DEPARTMENT OF BIOLOGY, TEXAS TECH UNIVERSITY, LUBBOCK, TEXAS 79409.
ACCEPTED 26 FEBRUARY 1974.

NEW LIFE MEMBER



Rosendo M. Fraga is now a Life Member of The Wilson Ornithological Society. Mr. Fraga is a graduate of the University of Buenos Aires, Argentina, and is a member of several biological societies. His interests in birds are in ecology, behavior, and evolution, and he has published in *The Auk*. He has wide interests in scientific subjects and in music, is single, and lives in Buenos Aires.

GENERAL NOTES

Age of first nesting in the Brown Pelican.—Disagreement exists in the literature as to the age at which Brown Pelicans (*Pelecanus occidentalis*) first breed. Bent (U.S. Natl. Mus., Bull. 121, 1922) and Palmer (Handbook of North American Birds, Vol. 1, 1962) say that breeding first occurs when the birds are about two years old, while others have suggested that this occurs at older ages. As no convincing evidence has been presented for any opinion, the question has remained unanswered (Henny, Bureau of Sport Fisheries and Wildlife, Wildlife Res. Report No. 1, 1972). We can now report from our studies on the Brown Pelican that marked individuals have first nested successfully when they were three years old.

In July 1968 a group of flightless, nestling pelicans was captured in a Florida colony and trucked to Grand Terre, Louisiana. There they were individually color-marked with patagial streamers similar to those described by Knowlton et al. (J. Wildlife Mgmt. 28:169-170, 1964), leg-banded, and released as part of a program to restore this recently extirpated species as a breeder in the "Pelican State." When released, the birds were 9 to 12 weeks old, and the older individuals were beginning to fly. Inventories of the color-marked, free-flying juveniles near the release area showed nearly 100 percent survival during the following months.

In late March 1971, 13 nests containing eggs were found on a low reef at the mouth of the Barataria Bay ship channel. Wing rivets, with remnants of the patagial streamers, and leg bands identified all the nesting birds as those released in the summer of 1968. At that time the nesting birds were almost three years old.

Additional Florida young were shipped to Louisiana in 1969, 1970, and 1971. These also apparently nested for the first time when they were approximately three years old. By 1973 so many banded pelicans with worn-out patagial streamers were present, along with the offspring from the 1971 and 1972 nesting seasons, that precise data on the ages of nesting birds were unattainable.

The nesting 3-year-olds were in an advanced subadult plumage. This is similar to the adult nuptial plumage, but it lacks the bright yellow crown and throat markings, has considerable white markings on the belly, shows a few dark marks on the crown, and has some light-colored markings on the neck (chestnut in full nuptial plumage). A light wash of yellow was first noticeable on the crown and median throat (through field glasses) at the start of the 1972 nesting season, when the older birds were nearly four years old. These markings did not become bright yellow (as they are in Florida nesting colonies) until 1974, when the older individuals were almost six years old.

One of us has visited all of the Brown Pelican colonies in Florida, some of them on several occasions, without finding substantial numbers of birds nesting in subadult plumage. The only exception was in a new colony of about 20 nests at Port St. Joe in 1972. Most of the breeding pelicans there were in subadult plumage similar to that worn by the 3-year-olds in Louisiana in 1968.

We do not consider ours to be the definitive statement on the age of first breeding in Brown Pelicans, nor do we believe that age of first breeding is necessarily a fixed parameter in the species. In some species, the age at first breeding is known to be lower when food is especially abundant and/or when older individuals have been removed from the population (Lack, Ecological Adaptations for Breeding in Birds, Methuen & Co., Ltd., London, 1968). Obviously, in 1968, the birds in our Louisiana colony contained no pelicans older than three years. Also, natural food supplies in the vicinity were such

that at least in the past thousands of pelicans were able to thrive there. In addition, natural food was greatly supplemented by large quantities of non-commercial fishes that were thrown overboard from the numerous trawlers returning to port. Similar circumstances existed at the Port St. Joe, Florida subadult-dominated colony in 1972.

Based on these observations, we believe that the age of first breeding in Brown Pelicans may be lower in new colonies than in established colonies. However, the species is clearly capable of successful breeding at three years of age.

This is in part a contribution of the Federal Aid to Wildlife Restoration Program, Florida Pittman-Robertson Project, W-41. We wish to thank Lawrence J. Blus and R. W. Schreiber for suggestions on the manuscript.—LOVETT E. WILLIAMS, JR., *Wildlife Research Projects Office, Florida Game and Fresh Water Fish Commission, Gainesville, Florida 32601* and TED JOANEN, *Refuge Division, Louisiana Wildlife and Fisheries Commission, Grand Chenier, Louisiana 70643, Accepted 10 May 1974.*

Aerial hunting by Little Blue Herons.—Aerial hunting methods have been described for several species of herons, including the Snowy Egret, *Egretta thula* (Kushlan, 1972); Louisiana Heron, *Hydranassa tricolor* (Kushlan, 1972); Great Egret, *Casmerodius albus* (Rodgers, 1974); Gray Heron, *Ardea cinerea* (Marshall, 1961); Great Blue Heron, *A. herodias* (Hedeon, 1967); and Yellow-crowned Night Heron, *Nyctanassa violacea* (Parmer, 1968). Diving from flight was briefly noted in Little Blue Herons, *Florida caerulea*, by Dickinson (1947) and Jenni (1969), but has not been described in detail.

In the period from late July to September 1972, I observed a total of 162 aerial dives by adult and immature Little Blue Herons during 11 periods of observation at the Welder Wildlife Refuge, San Patricio County, Texas. Such behavior was first noted on 26 July, although I had been studying Little Blue Heron feeding habits since April. Interestingly, the more typical Wade/Walk Slowly method of feeding (Meyerriecks, 1962) was not often observed during this July-to-September period.

Observations were made from a car using a 15-60X spotting scope. The herons dived and caught prey as close as 30 m from me, without indicating awareness of my presence. The sites of observation were at Encino and Pollito Lakes on the refuge. During late summer these lakes become covered with an opaque mat of vegetation, consisting of *Najas guadalupensis*, *Heteranthera dubia*, and green algae. The herons' activities were primarily at the edges of the lakes in areas of floating lotus (*Nelumbo lutea*) and tall, emergent grasses (*Paspalum* spp., *Panicum* spp.).

Aerial hunting behavior was variable in the herons, but typically it began with the bird flying from an elevated perch out over the lake, frequently banking sharply and emitting loud calls. In contrast to normal flight positioning, the neck was partially extended and the legs dangled. Before diving the heron usually hovered like a tern. The dive was performed feet-first, unless the bird was diving from five m or higher. In that case the bird plummeted head-first, righting itself just above the surface to enter the water feet-first. Frequently there was a last-moment directional change before the bird reached the water. As it contacted the water the heron speared its prey with a normal bill-thrust. If the water was too deep for standing, the bird swam on the surface; if the water was very shallow it might run a few steps as it struck. Hunting flights were usually brief and low, one to three meters above the water, though sometimes a dive was made from up to 10 m.

Ninety percent of the aerial hunts were accompanied by calls, during flying, hovering, or diving. These calls varied in tone, duration, and pitch, but may be represented as *croak* or *creek*. There are several possible functions for the calls. As the heron often made a directional change while diving, I suspect that frogs (the usual prey) might have reacted to the call, leaping as the bird descended. It is possible that such leaping would commit a frog to one direction of escape and improve the heron's chances of intercepting it. On the other hand, it has been reported that frogs exhibit "physical immobility and reduced responsiveness" when frightened by a noise (Nash et al., 1970; Boice and Williams, 1971). Perhaps the heron can effectively immobilize some prey by calling. Finally, the calling may also serve a social function, as the same calls typically are given during intraspecific chases about the feeding areas. Often several herons aerial-hunted on the same lake simultaneously, but in such cases they did not feed in close proximity; thus cooperative hunting seems highly unlikely.

Of the 25 identified prey items taken by aerial hunting, 23 (92 percent) were frogs (*Rana pipiens* and/or *R. catesbeiana*)—eight to 13 cm long, and two were small fish. This differs greatly from the diet obtained by Little Blue Herons using the common Wade/Walk Slowly method. From 4 April to 31 July I recorded 152 captures by the latter technique in adults and juveniles. Sizes estimates of each item, made through comparison with the heron's bill, showed the prey to be almost entirely fish and crayfish, with a mean body length of slightly greater than two cm. Using a length-weight curve plotted for 60 small fish trapped in the vicinity, I determined that the average prey item taken by wading weighed slightly less than one gram. By contrast, the aerial method resulted in the capture of frogs that were eight to 13 cm long and which weighed considerably more.

It was not possible to determine the result of all dives into vegetated areas, but of the 101 "scoreable" dives, 25 (25 percent) were successful in capturing prey. This is a much lower success rate per strike than that attained by the Wade/Walk Slowly method. My data show 152 captures out of 271 strikes (56 percent accuracy) for wading Little Blue Herons, and comparable figures derived from Recher and Recher (1969) show an accuracy of 58 percent. In my data on aerial hunting, adults (dark plumage) were not found more efficient than juveniles (white plumage)—and as demonstrated by Recher and Recher (1969) for wading hunting; however, my sample size is too small for proper analysis of this aspect.

Wading hunting is surely less energy-consuming and more accurate than aerial hunting, but it provides smaller prey. It is not known how much more energy is used in flying, so direct comparison of the overall efficiencies of the two hunting methods is not possible.

As aerial hunting was observed only in the late summer, it may involve certain advantages that disappear by late September. Several factors may be important: 1, the tadpoles of *Rana pipiens* and *R. catesbeiana* metamorphose in late summer into air-breathing, surface-dwelling adults (thus making a new food source potentially available to the herons); 2, these frogs tend to move into shallower water and generally swim poorly during the metamorphic process (Goodyear and Altig, 1971); 3, the vegetation mat becomes densest at that time of year, hiding the fish and thereby rendering this normal food source less accessible to the herons; 4, the aquatic grasses grow tall enough to render the newly-metamorphosed frogs inconspicuous to a wading but not to a flying heron; and 5, the lotus leaves reach peak development then, providing convenient but vulnerable places for frogs to bask in the sunshine. Aerial hunting was most common during dawn and dusk periods of the day, when frogs are most likely to be warming

themselves at the water's surface or on the lotus leaves (Brattstrom, 1963). The disappearance of aerial hunting in autumn is probably associated with the recession of the various forms of aquatic vegetation, the passing of the frogs from a particularly vulnerable phase in their development, and/or the frogs' dispersal from the vicinity. Aerial hunting, then, may be a behavioral adaptation for exploiting an ephemeral, large-item food source; or, it may be an alternate strategy that the herons must resort to when their usual food source is temporarily unavailable.

During this study I received financial support from an N.I.H. Training Grant (No. 5 TO1 GM01779) of the Department of Ecology and Behavioral Biology, University of Minnesota, and a research fellowship from the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas. Acknowledgment is made to Dr. Frank McKinney (University of Minnesota) for research advice and editorial assistance and to Dr. Clarence Cottam (Director, Welder Wildlife Foundation) for supervision and assistance in the field.

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- DOUGLAS W. MOCK, *Department of Ecology and Behavioral Biology, J. F. Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 55455. Accepted 11 April 1974.*

Use of artificial nest structures by Everglade Kites.—The Everglade Kite (*Rostrhamus sociabilis plumbeus*), a form now endangered in the United States, breeds regularly in the marshes on the west side of Lake Okeechobee, Glades County, Florida. In 1972 and 1973 about 80 percent of known U. S. nests were in this area. The nests are typically placed in cattails (*Typha domingensis*) and were in both those years. Of the



FIG. 1. The artificial nest structure for Everglade Kites showing details of the construction.

four nests observed there in 1972, two were blown down by high winds and the third was lost when invaded by ants (*Crematogaster atkinsoni*); the fourth nest fledged young. In 1973, some nests settled as much as 1 m, tipped over, and lost the contents. These nests were built in the taller clumps of *Typha*, above the main canopy of vegetation. The leaves of these taller cattails were too weak to support the weight of the nest, adults, and young or to withstand the effects of strong winds and driving rains.

From the above it is clear that kite nests are prone to misfortune, particularly due to high winds—which often accompany thunderstorms—and collapsing and shifting vegetation. In an effort to alleviate this problem artificial nest structures were used. In 1970 Ivan Sutton of Pleasanton, Kansas, designed and assembled two all-metal nest structures specifically for Everglade Kites. These he gave to the senior author, and since then several additional structures have been made.

In the spring of 1973, four Sutton nest structures were used for the first time. Into each an active nest was placed, and then the structure was set into place. Care was taken to insure that the nest remained at its original height and at the exact location as before. Only nests judged likely to settle, be blown down by high winds, or overturned by heavy rains were treated in this manner. As we suspect that kites will not initially build in these artificial structures—perhaps failing to recognize them as nesting sites, we waited until nest construction had been completed and one or more eggs laid before making the change.

The parent birds accepted and occupied the artificial structures in all four cases. At two nests the kites added material that increased the size of the nest after the switch was accomplished. When the initial changes were made, one nest contained young and three contained eggs. Two of the four nests were successful, fledging five young (two and three each). Failure of the other two nests resulted from predation on the eggs.

Although no ant problem was witnessed in 1973, use of artificial nest structures could greatly reduce this threat. This would be done by making the single vertical support ant-proof and by taking care to prevent surrounding vegetation from touching either the nest or the support structure. Additional modifications of the structure might also result in the prevention of nest predation by mammals and snakes.

The Sutton nest structure consists of a shallow basket attached to a 1.5-m-long shaft of thin-walled metal tubing (Fig. 1), 8 cm in diameter and open at the bottom end. The basket has a tubular outer ring, 1 cm in diameter, with six concentric and 15 radial strips, each 1.5-cm-wide and riveted together, forming the "nest." The basket measures 55 cm inside diameter and 8 cm in depth. It is supported on the bottom by three braces, which are woven into the basket and are attached by rivets to the main support tubing. The metal used in the construction is aircraft-grade 321-gauge stainless steel, but galvanized or aluminum sheet metal should be equally satisfactory. The concentric strips and the braces were cut from a sheet of the same gauge stainless steel, and the radials were cut from the upper end of the support shaft, leaving the lower ends attached. The support was inserted over a wooden post or metal pipe, each of the proper diameter to give a snug fit, and driven into the marsh substrate. The nest structure was found to be lightweight, durable, easy to handle in the field, and reusable indefinitely, if removed upon completion of nesting and stored in a sheltered place until ready for use at another nest.

We thank Ivan Sutton for making and delivering the nest structures at his own expense and to Reece I. Sailer and D. R. Smith, of the U. S. Department of Agriculture, Research Services, Beltsville, Maryland, for specific identification of the predator ants.—PAUL W. SYKES, JR., *Bureau of Sport Fisheries and Wildlife, Patuxent Wildlife Research Center, Field Station, P. O. Box 2077, Delray Beach, Florida 33444* and ROBERICK CHANDLER, *National Audubon Society, Sanctuaries Department, 505 SW 10th Street, Okeechobee, Florida 33472*. Accepted 6 May 1974.

Occurrence of Swainson's Hawk substantiated in New Jersey.—There are numerous sight and several specimen records of Swainson's Hawk (*Buteo swainsonii*) in the eastern United States, but apparently no previous substantiated records exist for New Jersey. The only specimen record from the state is of a bird purportedly collected in Essex County in 1915 (now in the Buffalo Museum of Science), but Heintzelman (Casinia, 54:31, 1973) has recently rejected it as being of doubtful validity.

On 16 September 1973, I trapped, banded, photographed, and released a light-phased juvenile ("immature") Swainson's Hawk at Cape May Point, Cape May County, New Jersey. Measurements were: wing (chord) 377 mm; culmen (from cere to tip of bill) 20.1 mm; and weight 518 g. The bird was in excellent plumage and showed no signs of having been in captivity. The primaries and rectrices (the tips of the latter still retained a small amount of down) were undamaged, whereas caged hawks nearly always damage the tips of these feathers. This species is not normally used for falconry and the tarsi showed no sign of wear by jesses. Thus I consider that this was a normal wild bird.

Photographs have been deposited in the National Photoduplication File, Patuxent Wildlife Research Center, Laurel, Maryland (accession numbers 342-1Ca and 342-1Cb). Mr. Chandler Robbins confirmed the species identification based on these photographs. This is Cape May Point Raptor Banding Station Research Report No. 2.—WILLIAM S. CLARK, 7800 Dasset Court, No. 101, Annandale, Virginia 22003. Accepted 19 March 1974.

American Kestrel transports Norway rat.—Adult *Rattus norvegicus* in northern Illinois have been found to weigh between 234 and 475 g (\bar{x} 372, based on 5 specimens). On two occasions I have observed a female American Kestrel (*Falco sparverius*) carrying what appeared to be an adult of this rat in its talons. Neither bird was more than 0.3 m above the ground when it flew in front of my automobile. One (NIU 1008) was struck by my car on 12 July 1959 near Belvidere, Boone County, Illinois. This female was carrying a rat from which portions of the thoracic region had been consumed. The rat was fresh and probably had been killed by the falcon. The second incident occurred on the same day near DeKalb, DeKalb County, Illinois. This kestrel was not collected, but flew in front of my vehicle in labored and close-to-the-ground flight.

Accurate weights are not available for representative female kestrels of the northern Illinois population, but birds from this area are probably larger than Oklahoma specimens for which I have weights (116.5 and 122.5 gms). However, even allowing for a few additional grams weight in Illinois birds, it appears that the American Kestrel is capable of flight while carrying prey approaching or perhaps twice its own body weight.

This paper represents contribution number 504 from the NIU Department of Biological Sciences.—WILLIAM E. SOUTHERN, Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115. Accepted 26 April 1974.

Recent breeding of the Sandhill Crane in North Dakota.—Before the present century, Sandhill Cranes (*Grus canadensis*) bred fairly commonly in North Dakota, but local breeding populations rapidly declined during the late 1800's and early 1900's (Stewart, Birds of North Dakota. In preparation). By the early 1920's this species had apparently been extirpated from the state as a breeding bird. On 22 June 1973 we obtained evidence of breeding in the state for the first time in recent decades. On that date we sighted a downy young crane accompanied by two adults. They were in a 130 hectare hay meadow, adjacent to the Souris River, on J. Clark Salyer National Wildlife Refuge, McHenry County. The area, interspersed with wetlands and subject to spring flooding in some years, is primarily vegetated with western wheatgrass (*Agropyron smithii*) and quackgrass (*A. repens*).

According to Littlefield and Ryder (Trans. 33rd North Amer. Wildlife Conf., 444-454, 1968), nests of the Sandhill Crane are normally located in or near free water. A search revealed the probable nest of the cranes, consisting of a pile of dried marsh vegetation (approximately 40 cm in diameter), surrounded by water. Eggshells were not present, but a crane feather was found near the structure.

We captured the young crane and estimated it to be 80 cm tall, with the primary quills erupted about 25 mm. Based on descriptions by Walkinshaw (The Sandhill Crane, Cranbrook Inst. Sci. Bull. 29, 1949), we estimated that the crane was approximately six

weeks old. On 26 June we last observed the young crane and adults in the meadow. Red-winged Blackbirds (*Agelaius phoeniceus*) were harassing the young bird, which struck and killed one, then walked out of view with the prey in its bill.—ROBERT C. FIELDS, ALAN K. TROUT, and DAROLD T. WALLS, *J. Clark Salyer National Wildlife Refuge, Bureau of Sport Fisheries and Wildlife, Upham, North Dakota 58789. Accepted 3 April 1974.*

Observations on the terrestrial wing displays of breeding Willets.—Willets (*Catoptrophorus semipalmatus*) are large tringine sandpipers with unusually prominent white wing stripes bordered with dark brown and black. They are monogamous breeders with each pair maintaining a nesting territory (Vogt, Proc. Linnean Soc. N. Y., 49:8-42, 1938) and sometimes a separate feeding territory (Tomkins, Wilson Bull., 77:151-167, 1965). Both authors attributed territory advertisement almost exclusively to males, which perform aerial displays and engage in partly ritualized border standoffs with neighboring males. Loud vocalizations are used in both situations. Both authors also commented on the conspicuousness of the wing pattern during precopulatory wing vibration and aerial hovering displays, the latter likened in function to passerine song by Vogt. They both believed that the contrasting pattern provided stimulation to the female during courtship. Other functions, such as species recognition and distraction, were postulated by Tomkins (op. cit.). No references were made to terrestrial wing displays other than precopulatory wing vibration. For this reason I report here observations I made on behavior of Willets near Corpus Christi, Texas, in March and April, 1973. These observations provide evidence of additional contexts in which terrestrial wing displays regularly occur.

The Willets in my study area rarely fed in the nesting territory, which was set off from Gulf waters by man-made dikes, but instead utilized nearby tidal marsh for that purpose. One member of each of four different pairs was color-marked. Two of these were determined to be males, on the basis of position in copulation and relative size and color pattern (males are smaller and more strongly marked than females). The sexes of the other two marked birds were not determined. One pair, of which the male was marked, maintained fidelity to the same feeding territory throughout the two-month period, while two other pairs showed only intermittent attachment to particular feeding sites. I monitored two pairs with adjacent, well-defined territories in the nesting area, and the males of both pairs were marked.

Terrestrial wing displays were observed in four contexts:

1. Prior to copulation males were observed to approach females from behind, extend the wings vertically, vibrate them and give a rapid, prolonged, staccato *kip-kip-kip*. . . call. This behavior has been described by Vogt (op. cit.) and Tomkins (op. cit.).

2. Males landing in either the nesting or feeding territory nearly always held both wings vertically for two to three seconds after alighting and gave the loud *pill-will-willet* call several times. As known females were not marked, it was not determined whether females perform the same display when landing alone in their territories. However, when both members of a pair landed together, the display was given by both simultaneously.

3. When conspecifics flew over or near a male Willet on its nesting or feeding territory, the latter usually responded by giving the *pill-will-willet* call, often accompanied by the partial or complete raising of both wings. I observed this response over 100 times and found that it could be reliably predicted when a flying bird was seen approaching. It was my impression that wing display occurring in this context was a direct function

of the proximity of the flying bird. I recorded only one such response by a female, which was alone on the nesting territory at the time. Occasionally the wing display was given without vocalization.

4. During encounters of two birds near a territorial boundary, each was observed to assume an upright posture with the tail spread and tilted toward the other bird as described by Vogt (op. cit.). The *kip-kip* call was usually given at a slow or irregular tempo and attack often followed. Although this display was commonly performed with the wings in normal position, I recorded several instances in which the wings were extended vertically.

Contexts 2 to 4 appeared to be directly related to advertisement or defense of territory, although an epigamic function could not be ruled out in 2. In 2 and 3 the message of territory occupancy is potentially communicated over long distances by virtue of the loudness of the *pill-will-willet* call. In 4 the call is more subdued and the target bird is nearby. As the great majority of wing displays occurred in conjunction with *pill-will-willet* calls (contexts 2 and 3), I believe that a main function of exposing the wing pattern is to reveal to distant conspecifics a bird's precise position after vocalization has attracted attention to a general area. In certain situations (context 2) the pattern helps attract the attention of any conspecifics in the area to a bird's arrival. In others (contexts 3 and 4) the displays are directed at specific targets. My own ability to locate calling birds was greatly enhanced if the wing pattern was exposed.

I was impressed with the high incidence and visibility of terrestrial wing displays in the Willet. Except for precopulatory wing displays, which are clearly epigamic, the literature provides only scanty evidence of territory-related wing displays in other tringines. *Limosa limosa* (Lind, Studies on the behaviour of the Black-tailed Godwit *Limosa limosa* L., Munksgaard, Copenhagen, 1961), *Tringa totanus* (Grosskopf, J. F. Ornith., 99: 1-17, 1959), and *T. solitaria* (Oring, Wilson Bull., 80:395-420, 1968) occasionally raise both wings during courtship or territorial defense. *Actitis macularia* uses a variety of wing-up displays in aggressive interactions (pers. obs.).

The literature contains much information on the wing displays of calidridine sandpipers, describing one-wing as well as two-wing displays in sexual and aggressive contexts. *Calidris alpina* (Holmes, Condor, 68:3-46, 1966), *C. melanotos* (Hamilton, Condor, 61:161-179, 1959), *C. maritima* (Bengtson, Ornis Scandinavica, 1:17-25, 1970), *C. mauri* (Brown, Ibis, 104:1-12, 1962), and *C. bairdii* and *C. fuscicollis* (Drury, Auk, 78:176-219, 1961) use vertical extensions of one wing during territorial encounters, usually with the underwing held facing the opponent. *C. temmincki* uses a two-wings up display, in combination with a trill, during courtship (Southern and Lewis, Brit. Birds, 31:314-321, 1938). *Tryngites subruficollis* exhibits a complicated repertoire of one- and two-wing displays in social gatherings (Oring, Auk, 81:83-86, 1964). Most species of sandpipers that use wing displays have the underwings white or show contrasting, light-dark wing patterns which accentuate the conspicuousness of the extended wing.

As the natural habitat of Willets lacks the elevated, conspicuous perches often used by many other species in the tringine group, selection may have favored the evolution of a more complex repertoire of wing displays and a more striking wing pattern as mechanisms for enhancing visibility. The same factor may account for what appears to be a greater diversity of wing displays (i.e., both one-wing and two-wing) among calidridines, most of which nest in open habitats; however, much more comparative information is needed to test this correlation.

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from the Penrose Fund of the American Philosophical Society. I would like to thank Alfred L. Gardner for critically reading an earlier draft of this manuscript and providing helpful comments and suggestions.—MARSHALL A. HOWE, *National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560. Accepted 1 March 1974.*

Breeding success relative to nest location and density in Ring-billed Gull colonies.—The role of nest location and density in determining breeding success in Ring-billed Gulls (*Larus delawarensis*), to our knowledge, has not been studied previously. In breeding colonies some nests will be located centrally while others are peripheral. Two factors that could affect breeding success of individual pairs within a colony are nest density and the relative location of each nest. Several workers have investigated nest location and its influence on breeding success of colonial breeding birds. Studies of the Black-headed Gull, *L. ridibundus* (Patterson, *Ibis*, 107:433-459, 1965), Adelie Penguin, *Pygoscellis adeliae* (Tenaza, *Condor*, 73:81-91, 1971), and the Black-legged Kittiwake, *Rissa tridactyla* (Coulson, *Nature*, 217:478-479, 1968), have shown that birds nesting solitarily, or on the edge of colonies, tend to have lower reproductive success than those nesting in the colony center.

We studied two Ring-billed Gull colonies in Lake Huron from 16 May to 4 July 1972. The Calcite Colony is located on a man-made peninsula near Roger City, Presque Isle County, Michigan. The other colony is on Bird Island in Thunder Bay near Ossineke, Alpena County, Michigan. The Calcite Colony contained about 3,000 pairs of nesting Ring-billed Gulls and is situated along the south shore of the proximal portion of the peninsula, about 2 m above water level. The ground is generally level and in summer it is partially covered with low-growing (1 m high) herbaceous vegetation, mostly grasses and a few burdock (*Arctium* sp.).

During highs in the Great Lake water cycle, such as when our study was conducted (see monthly and yearly mean water levels, Chart No. 207, Department of the Environment, Ottawa, Ontario), Bird Island is actually three small low-lying islands. We conducted our observations on the middle islet, which had approximately 500 nesting pairs of Ring-billed Gulls. Dense brush (1 to 7 m high) covered the islet except for portions of the south and east sides, which were essentially without vegetation and had the most gull nests. The most abundant plant species were red-osier dogwood (*Cornus stolonifera*), green ash (*Fraxinus pennsylvanica*), arbor vitae (*Thuja occidentalis*), and 2 m high nettle (*Urtica gracilis*).

For our study we used 184 nests in the Calcite Colony and 315 nests in the Bird Island Colony. Only those nests that formed the interface between the colony and its surrounding environment were considered as constituting the fringe sample. Nests proximate to the geometric center of each colony were selected as representative of the center. Nest density was measured by counting all contemporary nests within a radius of 1 m of each nest cup.

We visited the study sites at least every other day and recorded the number of eggs and young present, any mortality in each nest, and weather conditions. Data were collected on chicks from the time of hatching until they were 21-days-old or dead, whichever might have come first. The term "breeding success" is used here as a combination of hatching success and chick survival through 21 days.

Two statistical tests were applied to the data. For examining the effects of nest loca-

TABLE 1

BREEDING SUCCESS IN CENTRAL AND FRINGE AREAS OF RING-BILLED GULL COLONIES

| Nest location | No. of nests | No. of eggs | No. eggs hatched | No. chicks surviving | No. "successful" chicks |
|--------------------|--------------|-------------|---------------------|----------------------|-------------------------|
| Calcite Colony | | | | | |
| Fringe | 42 | 115 | 63 | 51 | 51 |
| Center | 38 | 111 | 79 | 72 | 72 |
| χ^2 | | | 5.150 ² | 2.321 | 8.753 ² |
| Bird Island Colony | | | | | |
| Fringe | 65 | 173 | 77 | 44 | 44 |
| Center | 42 | 119 | 97 | 77 | 77 |
| χ^2 | | | 42.463 ³ | 8.651 ² | 43.205 ³ |

¹ Survival to 21 days.

² Significance at five percent level.

³ Significance at one percent level.

tion on breeding success, we used 2×2 contingency table analysis with the Yate's correction for continuity (χ^2_c). To determine if breeding success was correlated with nest density, we used the Kendal rank correlation analysis (Siegel, Nonparametric statistic for the behavioral sciences, McGraw-Hill Book Co., Inc., 1956). The five percent significant level was employed in both cases.

Table 1 shows the results of the statistical analysis of breeding success depending on nest location. Both colonies showed a significantly higher hatching rate for pairs nesting in the center of the colony than those on the fringe. Chick survival in the Calcite Colony did not differ significantly between the center and the fringe; however, on Bird Island there was a significant difference, favoring survival at the center. As these results were based on one season's work, they can not be considered conclusive. It appears, however, that nest location in perspective with topographical features does affect Ring-billed Gull breeding success. Lower hatching rates at the fringe are primarily responsible for the difference.

Several factors, singly or in combination, may contribute to lower hatching success and chick survival at the fringe. Birds of comparable reproductive experience and capabilities may not be distributed equally throughout the colony, and the fringe territories may be inhabited by a larger proportion of gulls breeding for the first time. Also nests along the colony fringe may be located in areas subject to wave action during high winds. At Bird Island, waves destroyed nests and caused extensive wetting of eggs and chicks. When the chicks were between one and two weeks old, wave action eroded about 2.5 m of shoreline and damaged many nests along the fringe. In contrast, the Calcite Colony was not affected by high water because of its elevation. This is probably a primary reason for the difference between chick survival rates at the two colonies.

There was no correlation between nest density and breeding success for Ring-billed Gulls nesting within either colony (Kendal's rank correlation coefficient, Calcite Colony = 0.29; Bird Island Colony = 0.29). This does not infer that density dependent factors (e.g., social releasers) are unimportant in the successful nesting of this species. Instead, it simply means that nearness of neighbors (i.e., closeness of territories) had no direct bearing on nesting success within the colony.

We would like to express our appreciation to the U. S. Steel Corporation Michigan Limestone Division for permitting us to conduct our studies on their property, Mr. T. Mears of Alpena Community College for use of a motor boat, and Dr. J. Zar of NIU for providing statistical advice. The project was conducted while Dr. Southern was under support from National Science Foundation Contract GB 28856. This paper is contribution number 503 from the NIU Department of Biological Sciences.—MARILYN DEXHEIMER and WILLIAM E. SOUTHERN. *Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115. Accepted 25 April 1974.*

Use of abandoned cacique nests by nesting Troupials (*Icterus icterus*): precursor to parasitism?—On 16 September 1971, I observed five individual Troupials (*Icterus icterus croconotus*) investigating and entering disused nests of Yellow-rumped Cacique (*Cacicus cela*) along 20 km of the Río Jivino near Limoncocha, Ecuador (0° 24' S; 76° 38' W). The cacique nests were clustered together in trees overhanging the river, usually 5 to 15 nests per cluster. By 10 October, each pair of Troupials had obviously selected a nest and was repairing and using it for its own. In no case did I see more than one pair of Troupials using a given cluster of cacique nests. Along a small river at Tumi Chucua, Bolivia (11° 8' S; 66° 10' W), I observed the same kind of behavior in October and November 1972. At neither locality did I see evidence that Troupials constructed their own nests. I can find no reference to the nests of the southern race of the Troupial (*I. i. croconotus*). Phelps (Aves Venezolanas, Creole Petroleum Corp., Caracas, 1953) states that individuals of the northern race (*I. i. icterus*) occasionally construct their own nests in the form of a bag, but generally they repair and use old nests of other species.

In taking over abandoned cacique nests, the Troupial could be evolutionarily moving into an ideal set of circumstances for developing brood parasitism, at least in the Limoncocha and Tumi Chucua areas. Both the potential host and the potential parasite species are icterids feeding almost entirely on insects during the breeding season. The Troupial was rare compared to the Yellow-rumped Cacique, the latter being among the 10 most common species while the Troupial was more than 100th in rank of commonness. The potential host is a colonial nester, and its nesting was synchronized within a period of three months at both sites.

By using the old cacique nests, the Troupial saves a considerable investment of time and energy in repairing rather than completely constructing a nest. Furthermore, the cacique nests themselves may be attractive in that: 1, they are frequently located in trees along rivers, the foliage of which is the principal foraging area of the Troupial; 2, the nests are often in the vicinity of wasp nests, which presumably protect the young caciques and orioles from botflies and predators (Smith, *Nature* 219:690-694, 1968); 3, the nests are at the ends of branches and difficult for many potential predators to approach; and 4, the nests are clustered tightly together, which may act as a maze in deterring predators, i.e., a potential predator has a much greater chance of finding several empty nests in a cluster before discovering the single nest containing Troupial eggs or young.

If behavior were to develop in which the Troupial were to investigate clusters of nests before the caciques were through laying eggs, if the Troupial were to advance its egg-laying cycle to correspond with that of the caciques, and if the Troupial were to develop egg-dumping behavior, then brood parasitism could evolve in the species. On the other hand, few, if any, brood parasites are as gaudily colored as the Troupial (black

and bright orange in both sexes), and one would expect selection for less obvious plumage as the evolution progressed toward the advanced stages of parasitism. As an alternative to less bold coloration, one might predict selection for a coloration—at least in the female Troupial—mimicking that of the Yellow-rumped Cacique. In terms of song, a form of mimicry already exists, but in this case it is the cacique that is the mimic. Yellow-rumped Caciques will mimic almost any loud and distinct noise or song, and this includes the loud, clear, double-noted whistle that the Troupial monotonously sings. This mimetic behavior could facilitate approach of the Troupial to the active Yellow-rumped Cacique colony.

Brood parasitism has evolved independently in several families of birds. Hamilton and Orians (Condor 67:361-382, 1965) have discussed possible theories explaining the evolution of this phenomenon and have developed a list of general characteristics they believed most appropriate for a species to potentially evolve parasitic behavior. Among these characteristics for early stages of brood parasitism were: 1, the evolving species should parasitize closely related species to best ensure appropriate food for the young; 2, the potential parasite should be relatively rare with respect to the potential host, to minimize selective pressure for anti-predator devices in the host species; and 3, the host species should most likely be a colonial nester, both for easy location of nests by the parasite and because the weaker territorial tendencies of colonial species increases the possibility of access to the nests.

From these characteristics, the Troupial could be considered an example of a species potentially in the early process of developing brood parasitism. This is not to say that all or even most species that use the abandoned nests of other species are apt to become parasites. For example, the Pirate Flycatcher (*Legatus leucophaeus*) (Haverschmidt, Birds of Surinam, Oliver and Boyd, London, 1968) and the White-ringed Flycatcher (*Conopias parva*) (Haverschmidt, Auk 90:207-208, 1973) have been recorded using old Yellow-rumped Cacique nests. These species, however, do not appear to combine as broad a spectrum of preadapted characteristics to evolve brood parasitism as the Troupial.

Herbert Friedmann and Dennis R. Paulson critically reviewed early manuscripts of this article and National Science Foundation Grant GB-20978 provided partial support for the field work.—DAVID L. PEARSON, *Department of Zoology, University of Washington, Seattle, Washington 98195. Accepted 20 April 1974.*

Rusty Blackbirds prey on sparrows.—Harsh weather or other conditions that produce food shortages may cause non-raptorial species to become predatory on other birds. Reports of such instances are not common, but included among the species one might list the Roadrunner (*Geococcyx californianus*), Common Grackle (*Quiscalus quiscula*), jays of various species, and even the Brown-headed Cowbird (*Molothrus ater*) (Roth, Condor, 73:113, 1971). In the spring of 1972, during a cold snap, several instances of predation on birds by Rusty Blackbirds (*Euphagus carolinus*) was witnessed at Fort Good Hope, Northwest Territories. The species attacked were Tree Sparrows (*Spizella arborea*) and White-crowned Sparrows (*Zonotrichia leucophrys*), and a Lapland Longspur (*Calcarius lapponicus*) was seen being eaten by a blackbird. Also, Mew Gulls (*Larus canus*) were observed eating birds of some of these species, although whether this was predation or scavaging is unknown.

When we arrived at Fort Good Hope on 4 May, standing waters were still frozen, but the snow cover was quickly disappearing and patches of bare ground existed throughout the settlement. Spring migrants arrived during the first week of May: White-crowned Sparrows on 5 May, Tree Sparrows and Lapland Longspurs on 7 May, Rusty Blackbirds on 12 May, and Mew Gulls on 17 May. Weather during the first three weeks of May was generally sunny and clear but cold. Flocks of up to twenty sparrows and longspurs were scattered throughout the settlement, feeding in patches of exposed vegetation, while Rusty Blackbirds frequented riparian habitats. Mew Gulls flocked over narrow channels of open melt water along the Mackenzie River. No interaction between these birds was noticed until later in the month when a cold snap occurred in the area. Light snow flurries commenced during the late afternoon of 21 May, becoming heavy but intermittent during the night and the following day. It was evident on the morning of 22 May that migrant passerines had been forced into the settlement by the blizzard, as aggregations of up to 200 birds gathered in the lee of buildings where some vegetation remained exposed. We estimated that at least 500 White-crowned Sparrows foraged in the area adjacent to our trailer on 22 May, 800 on 23 May, and 600 on 24 May, along with a few Tree Sparrows, Lapland Longspurs, Rusty Blackbirds, and Mew Gulls.

On 22 May we established a ground feeder near our trailer with oats, wheat, flax, cornmeal and bread. No aggressive behaviour between birds at the feeder was noticed until the afternoon of 23 May. At 17:46 an adult male Rusty Blackbird was watched by M. G. Shepard, walking towards the feeder where 42 White-crowned Sparrows were busily feeding. When about five feet from a sparrow, the blackbird attacked and grabbed it by the nape. N. K. Dawe then observed the blackbird standing on its prey, holding it by the breast with its feet. Several feathers were plucked from the sparrow's breast before the blackbird flew to nearby trees about 20 yards away, leaving its prey behind. The sparrow flew to a nearby snow pile at the edge of the road, where it died within minutes. The blackbird returned to the dead sparrow twice, both times hovering over and trying to pick it up with its bill. On the third effort, the blackbird lifted the sparrow and carried it about eight feet, before dropping it in the middle of the gravel road. Three more times the blackbird tried to pick up its prey and fly off with it. Unfortunately a truck frightened the blackbird away at 17:59. We retrieved the sparrow carcass for examination and noticed a break in the skin, along the middle of the upper back, about one inch by five-eighths inch. We assumed the sparrow died by chilling. It was a male and weighed 20.0 grams.

At 18:10 a tailless White-crowned Sparrow was seen at the feeder, perhaps the victim of a blackbird attack. Five minutes later a male Rusty Blackbird came to the feeder, and in 15 minutes it unsuccessfully attacked three White-crowned Sparrows and a Tree Sparrow. At 18:40 a female blackbird appeared at the feeder, attacked and pecked to death a White-crowned Sparrow. The blackbird flew off leaving its prey. Within six minutes the other sparrows had returned to feed, even though the carcass of the sparrow lay nearby. An adult Mew Gull, recently arrived at the feeder, showed no interest in the carcass but fed on cubes of bread.

From 18:40 to 19:10 two Rusty Blackbirds fed on cereals and bread at the feeder with the sparrows, and at 19:13 a blackbird made a last unsuccessful attack on sparrows. At 19:14 an adult Mew Gull picked up a dead White-crowned Sparrow from the road and swallowed its head first.

In addition to the feeder observations, two aerial chases of White-crowned Sparrows by Rusty Blackbirds were witnessed. In both instances, a blackbird left a tree to swoop down on sparrows feeding under or near spruce trees. Both attacks were unsuccessful.

The following day, on 24 May, a male Rusty Blackbird was seen feeding on a White-crowned Sparrow near the feeding station. When finished, all that remained of the sparrow was the wings and tail. On the same day, Mew Gulls were twice seen feeding on White-crowned Sparrows. In the first case a dead sparrow was picked up by the head and shaken vigorously for a second or two. The carcass was dropped and then picked up and shaken again. This action was repeated twenty-two times before the gull finally swallowed the sparrow. In the second instance, involving a sparrow killed by a passing truck, the gull picked up the dead bird and swallowed its head first on a single try.

The only other observation of possible predation was recorded at Norman Wells on 25 May, where an adult male Rusty Blackbird was flushed from a carcass of a male Lapland Longspur on which it was feeding. The carcass had been opened entirely from the midback to the throat. The neck had been eaten as well as the brain.

In summary, Rusty Blackbirds attacked White-crowned and Tree Sparrows during a three day cold snap, successfully killing two White-crowns. A blackbird was also seen feeding on a Lapland Longspur and Mew Gulls on White-crowned Sparrows, but by what these birds were killed was not determined.

This paper arises from field research undertaken on behalf of the Environment Protection Board for Canadian Arctic Gas Study Limited during the summer of 1972.—R. WAYNE CAMPBELL, *British Columbia Provincial Museum, Victoria, British Columbia, Canada. Accepted 4 March 1974.*

Variation in the Olive Sparrow in the Yucatan Peninsula.—The Yucatan Peninsula of Mexico, British Honduras and northernmost Guatemala is well known as a major center of endemism in Middle American birds. Many species are also represented by endemic races on one or more of the islands adjacent to the peninsula. Only about a score of species show geographic variation at the subspecies level within the peninsular mainland (Paynter, Peabody Mus. Nat. Hist., Bull. 9, 1955). Most of these are represented by an endemic Yucatan race, plus another that ranges from elsewhere in Middle America into the more humid base of the peninsula, i.e., southern Campeche, southern Quintana Roo, the Petén of Guatemala, and British Honduras. In one species, the Black-throated Bobwhite (*Colinus nigrogularis*), two endemic peninsular races are recognized: a pale one confined to Paynter's (op. cit.:14-15) "Scrub" zone of the extreme north, and a dark one in the adjacent "Deciduous Forest" zone to the south.

Study of some fifty Yucatan Peninsula specimens of the Olive Sparrow (*Arremonops rufivirgatus*), virtually all in fresh plumage, has shown that this species exhibits a pattern of differentiation like that of the *Colinus*. The type locality of the presently recognized Yucatan endemic subspecies, *A. r. verticalis* (Ridgway), is Mérida, in the Deciduous Forest zone. The undescribed race of the Scrub zone may be called:

***Arremonops rufivirgatus rhyptothorax*, ssp. nov.**

Holotype.—Carnegie Museum of Natural History (CM) No. 141994, adult ♂, collected 12 January 1965 by R. W. Dickerman, 5 to 6 km. E of Chicxulub Puerto, Yucatan, Mexico. Original number K. C. Parkes 2056.

Diagnosis.—This new race differs from *A. r. verticalis* (Ridgway) in its generally paler coloration. The underparts in *rhyptothorax* are much whiter, relieved only by a pale gray breast band, which is scarcely visible in some birds. In *verticalis* only the mid-

abdominal region is pure white; the breast band is ashy or even slightly brownish gray, and the throat, although whiter than the breast band, is usually somewhat grayish. In *verticalis* the gray color of the breast band continues along the flanks, becoming mixed posteriorly with dull green. In *rhypthorax* the pigmented area of the flanks is narrower, paler, and mixed posteriorly with ashy brown rather than green. The under tail coverts of *verticalis* are of a somewhat variable pinkish buff; in *rhypthorax* they vary from a paler version of the same color to virtually pure white. The upperparts of *rhypthorax* are also paler and grayer than those of *verticalis*: the dorsum and tail are less richly green, and in some fresh-plumaged specimens there is a distinct gray wash on the green on the back. The gray of the face and mid-crown of *rhypthorax* is paler and purer (less brownish) than in *verticalis*. The brown of the crown stripes averages brighter and more rufous, although this is individually variable; in general, less contrast exists between the stripes and the mid-crown in *verticalis* than in *rhypthorax*. Wing and bill length do not differ, but the bill of *verticalis* gives the distinct impression of being somewhat more swollen or inflated than that of *rhypthorax*.

Etymology.—From the Greek *rhyptho*, to wash or remove dirt, and *thorax*, chest, in reference to the "cleaner" look of the underparts.

Range.—Confined to the narrow belt of coastal scrub of the northernmost Yucatan Peninsula, Mexico (see below for remarks on intergradation with *verticalis*).

Discussion.—The narrow coastal scrub belt of Yucatan is highly distinctive (see photographs in Paynter, op. cit.:pl. 1). Except for coconut (*Cocos nucifera*) plantations, the maximum height of the woody vegetation is about three meters, and in much of the area the cover is thin and sparse. This coastal belt is exceedingly arid, with 428 mm mean annual rainfall at Progreso, compared to 901 mm at Mérida (Paynter, op. cit.: 10), which is only about 36 km inland and in the northern portion of the Deciduous Forest zone. The coastal zone coincides approximately with a sandy barrier beach, usually separated from what I shall call the "mainland" by (depending on locality) open water, marshes, mangrove swamps, savannah, and salt flats; in some places there is more or less continuous scrub. The resident avifauna of the coastal scrub is depauperate but distinctive. The wren *Campylorhynchus yucatanicus* is endemic to this zone, and the peninsular populations of several other species (*Zenaida aurita*, *Doricha eliza*, *Polioptila albiloris*) are almost completely confined to it.

Although the coastal strip is separated from the mainland by unsuitable habitat along most of its length, some gene flow appears to occur between coastal and mainland populations of both *Colinus nigrogularis* (Paynter, op. cit.:81) and *Arremonops rufivirgatus*. In the latter species, a series of 10 specimens taken at localities along the Progreso-Mérida highway, between 3.2 and 14.6 km south of Progreso (the last locality being about 21 km north of Mérida, type locality of *verticalis*), shows a rather rapid shift in color. Three of the four specimens from the southernmost of these localities are indistinguishable from *verticalis*: the fourth (RWD 11611) is noticeably paler and grayer. Specimens from between 3.2 and 5 km south of Progreso are nearest *rhypthorax*, although taken on the mainland, and those from 10 to 10.5 km south of Progreso are variably intermediate.

Paynter (op. cit.:294) stated that *verticalis* is "apparently isolated from other populations [of the species] by a barrier of high, wet forest." There are no populations of *A. rufivirgatus* directly south or southeast of the range of *verticalis*. In the southern and southeastern parts of its range, *verticalis* is sympatric with *A. chloronotus*, the more typically rain forest inhabiting species of the genus. Within the rain forest zone, *A. r.*

verticalis appears to be confined to cleared and second-growth areas. Most of a good series of fresh-plumaged specimens that I examined from the vicinities of Chetumal and Felipe Carrillo Puerto, Quintana Roo, do not differ from topotypical *verticalis*. At least three specimens (RWD 12670, 12671; CM 142182), however, taken on 31 January 1965, 6.5 km south of Felipe Carrillo Puerto, appear to represent *A. rufivirgatus* × *A. chloronotus* hybrids. I have seen one of the two British Honduras specimens listed by Russell (Ornith. Monogr. 1:182, 1964). This specimen (CU 29215) is badly worn, but appears to be typical of *A. r. verticalis*.

To the southwest, the range of *verticalis* is widely separated from that of *A. r. chiapensis* Nelson of central Chiapas. To the west, the range of *verticalis* approaches, without any obvious habitat barrier, that of *A. r. crassirostris* (Ridgway), which extends south-eastward to southern Veracruz. The latter race is distinguished from the Yucatan races by, among other things, paler, redder brown crown stripes with black shaft-stripes reduced or absent; mid-crown green rather than gray; and the throat, breast and flanks washed with rich buffy brown rather than gray. In spite of the alleged isolation of *verticalis*, evidence of intergradation between that race and *crassirostris* does exist. Four specimens (3 CM, 1 UMMZ) from Ciudad Campeche and Champotón, Campeche, from the southwestern corner of the range of *verticalis* (and west of the westernmost locality from which Paynter had specimens), are rather variable. The gray of their mid-crowns is variably washed with green. One specimen (CM 143254) has bright rufous crown stripes, virtually lacking black shaft-stripes except on the forehead portion. In the other three, the crown stripes are browner than in any of the series of Yucatan *verticalis*. Although the anterior underparts are like those of *verticalis*, the flanks of all four are mixed posteriorly with a browner, less green color than in true *verticalis*.

The best evidence of intergradation between *verticalis* and *crassirostris* is afforded by the one known specimen from Tabasco (LSU 24197). The intermediacy of this specimen, from ca. 18 km north of Balancán, easternmost Tabasco, has already been mentioned by Monroe (Occ. Pap. Mus. Zool. Louisiana State Univ., 28:7, 1963). In addition to "having the gray crown stripes more olive than in any other *verticalis* specimen," the only character cited by Monroe, the gray of the face, underparts and flanks of the Tabasco specimen shows a noticeably brown tinge, and the crown stripes are brighter and more reddish than in typical *verticalis*. Careful searching in other areas of Tabasco may well reveal populations of *A. rufivirgatus* narrowing the remainder of the apparent gap between *crassirostris* and *verticalis*.

Acknowledgments.—Drs. Robert W. Dickerman and Allan R. Phillips kindly made special efforts to secure specimens for this study during our joint collecting trips to the Yucatan Peninsula. The Dickerman (RWD) specimens will be deposited in the James Ford Bell Museum of Natural History (University of Minnesota), Cornell University, and American Museum of Natural History, and those of Phillips in the Delaware Museum of Natural History. I am indebted for specimen loans also to the curators of the Peabody Museum of Natural History, Yale University; Museum of Zoology, Louisiana State University (LSU); Museum of Zoology, University of Michigan (UMMZ); and Cornell University (CU). My collecting activities in Mexico were supported by the Edward O'Neil Fund of Carnegie Museum of Natural History. Permits to collect birds were obtained through the Departamento de Conservación de la Fauna Silvestre, and most specimens from our Yucatan expeditions were prepared by Juan Nava S. and Santos Farfán B.—KENNETH C. PARKES, *Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213. Accepted 30 April 1974.*

A stochastic model of leaf-scratching bouts in two emberizine species.—After having emphasized the need for more careful study of the two-footed leaf-scratching by emberizines (Hailman, *Wilson Bull.*, 85:348–350, 1973), I noticed an apparent difference in scratching behavior of two species, Dark-eyed Juncos (*Junco hyemalis*) of the Slate-colored form seemed to scratch only once, whereas White-throated Sparrows (*Zonotrichia albicollis*) frequently appeared to scratch twice. Therefore, I made a quantitative observational study, the results of which led to a model that may explain bouts of multiple scratching in general, as well as the nature of species-differences.

In order to accumulate sufficient data under relatively constant conditions, I baited the ground under my study window in Madison, Wisconsin. Each day during October and early November 1972, I scattered approximately one measuring cup of mixed bird seed over an area about 1×2 m, which is shaded by various planted bushes and trees that provide a leaf-litter over patches of bare earth and grasses. Birds visiting the feeding area are all presumed to be migrants, since neither juncos nor sparrows visited our feeding station during mid-winter. I saw as many as six juncos and as many as eight Whitethroats feeding at one time, as well as a few individuals of other emberizine species, but have no way of estimating the total numbers of individuals in the area.

I noted each scratching bout observed as being single or multiple: if multiple, I recorded the number of individual scratching motions given in succession. There is the possibility of observational bias in judging the difference between spaced single scratches and multiple scratches. If the animal noticeably paused between two movements, or made any other intervening action, the observation was recorded as two single scratches. Simultaneous judgments made on the same bird by another observer revealed complete agreement with my notes, so that bias in judgment is probably a relatively small factor in the results.

Nearly 500 single or multiple scratching bouts were recorded under these conditions: 250 from juncos and 229 from Whitethroats. Both species most frequently scratched singly: 68 percent of junco bouts and 62 percent of Whitethroat bouts. However, juncos did engage in multiple scratching, with as many as five consecutive motions, whereas multiple scratches of Whitethroats were as high as seven scratches per bout.

Since the data indicated a quantitative rather than qualitative difference between the two species, it was necessary first to understand how the number of scratches per bout was determined in either species. Biological variation is often Gaussian-like: evolution selects for an average value and there is variation around that average. In this case, however, the modal value is one scratch per bout and variation is necessarily constrained to higher values. I propose to explain this peculiar case of behavioral variation by operationally distinguishing between a "successful" scratch that is not followed by another scratch in the same bout and an "unsuccessful" scratch (failure) that is immediately followed by another scratch. After presenting the model and the data I offer a possible explanation of how "success" is determined in controlling behavior.

Suppose q is the probability that a given scratch in a series is successful, where successful means the bird halts scratching, perhaps to inspect more carefully the area at its feet or to feed. The probability of an unsuccessful scratch is therefore $p = 1 - q$, where p is the probability of performing another scratch without halting. If this probability of failure is independent of the number of scratches the bird has already performed in the bout (that is, p is constant), then a tight logical deduction can be drawn that predicts the nature of the frequency distribution of scratches/bout.

Let s stand for the number of scratches/bout, and B for the total number of bouts observed. The frequency of bouts having at least one scratch (f_1) is clearly B . The fre-

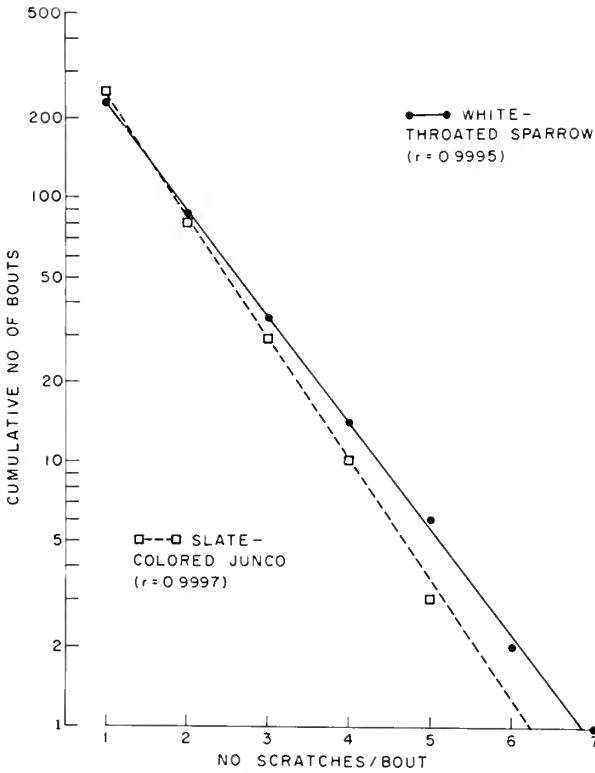


Fig. 1. "Geometric decay" curves of leaf-scratching for two species, in which the logarithm of the cumulative frequency is plotted against the number of successive scratching motions per bout. The least-squares fit of straight lines with high negative correlation coefficients (r values) indicates that the number of scratches per bout is "random" (see text). The slightly shallower slope of the Whitethroat line reflects a slightly higher probability of multiple-scratching.

quency of bouts having at least two scratches is the probability of failure on the first scratch (p) times the number of bouts having at least one scratch (B), so that $f_2 = pB$. The frequency of bouts having at least three scratches (f_3) is the product of the probability of failing on the second scratch (still the constant p) and the number of bouts having at least two scratches (pB), so that $f_3 = p(pB) = p^2B$. Clearly this sequence generalizes to

$$f_s = p^{s-1}B, \tag{1}$$

where s is the number of scratches/bout and f_s is the frequency of bouts having at least s scratches. (In other words, f_s is a cumulative frequency, empirically arrived at by summing the frequencies beginning with the highest value of s and accumulating "backwards.") Note that when $s = 1$, $p^0 = 1$, so that $f_1 = B$. Taking the logarithm of both sides of equation (1), we obtain

$$\log f_s = (s - 1) \log p + \log B, \tag{2}$$

an exponential equation in which $\log f_s$ is linearly proportional to $s-1$ (and hence also to s), with slope $\log p$ and intercept $\log B$. Since the logarithm of a fraction (p) is always negative, the slope is negative. In short, if the probability of adding another scratch to a bout is constant and independent of the number of scratches already performed, then the logarithm of the frequency of bouts having at least s scratches is inversely proportional to s , the number of scratches/bout.

It may help intuitively to point out that this simple model is related to the survivorship curves of banded birds of a single year-class where mortality is constant through time, and to the decay of radioactive materials—except that scratching is a discrete variable (number of scratches per bout), whereas time is a continuous one. The model may thus be termed a “geometric decay function” in parallel with the exponential decay functions of demography and radioactive disintegration.

Figure 1 shows the graphic analysis for both species. The fit of the data to a straight line (geometric decay function) is close: negative correlation coefficients exceeding 0.999 were found for both species. The lines fitted to the data in Figure 1 are lines of least-squares regression, and it will be noted that the slope of the junco line is slightly steeper than that of the Whitethroat. Since slope expresses the probability of adding another scratching motion in a bout according to equation (2), the difference in slopes shows that Whitethroats do in fact have a slightly higher probability of multiple scratching than do juncos.

My conclusion from these results is that both species possess fundamentally the same kind of scratching behavior. The most parsimonious interpretation of the geometric decay functions is that the effectiveness of a scratch in a bout is assessed visually during scratching: the decision as to whether to scratch again before pausing to inspect for seeds is made very rapidly so that no break in the scratching motions is necessary. Indeed, birds often appeared to be looking down while scratching. Finally, the small quantitative difference between the two species might be due to several factors, such as differences in visual criterion of a “successful” scratch or differences in preferred foraging habitat.

It is my impression that the last factor may be operating, for the Whitethroats appear to pick scratching sites more heavily leaved than sites picked by juncos. Therefore, a Whitethroat scratch will have a slightly lower chance of successfully clearing the ground of leaves, and consequently performance of a successive scratch will be slightly more probable.

I thank B. Dennis Sustare and Edward H. Buitt for very helpfully criticizing the manuscript despite their sharing my bias that quantitative explanations of even “simple” behavioral patterns can yield interesting results.—JACK P. HAILMAN, *Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706. Accepted 28 February 1974.*

Breeding range extensions of certain birds in New Mexico.—During field work in 1971–1973 at Tucumcari and in the Rio Grande Valley, New Mexico, I obtained the following notable extensions in the ranges of breeding birds in the state.

White-faced Ibis (*Plegadis chihi*).—On 16 June 1973, Ms. Barbara Escher and I flushed an adult White-faced Ibis from its nest at Tucumcari Lake, just east of Tucumcari, Quay County. The nest was built among cattails (*Typha* sp.) in the midst of a Black-crowned Night Heron (*Nycticorax nycticorax*) heronry. The night heron

nests were empty or contained young about to fledge. The ibis nest, made primarily of cattails, was built up about 18 inches above the water. It contained four blue or blue-green eggs, of which I obtained several photographs.

Plegadis chihli is a statewide migrant and occasional in summer and winter in New Mexico, but it has not been previously reported nesting in the state (Hubbard, checklist of the birds of New Mexico, New Mexico Ornithol. Soc. Publ., 3:13, 1970). Its breeding at Tucumcari Lake is somewhat unexpected, although this site supports an interesting breeding array of aquatic species in a region otherwise dominated by plains and other arid habitats. The lake itself, occupying a depression between U.S. Highways 66 and 54, is a generally shallow sheet of water of several hundred acres extent. Marshes of cattail and rushes (*Scirpus* sp.) are widespread, interspersed with open water and bordered by varied shoreline habitats.

Black Hawk (*Buteogallus anthracinus*).—On 25 July 1971, I found three of these hawks at the nest in woodland along the Rio Grande, near Alameda, Bernalillo County. The overstory was cottonwood (*Populus wislizenii*), with an understory of salt cedar (*Tamarix* sp.) and Russian olive (*Elaeagnus angustifolia*). One adult bird was clearly seen, and an immature flew from the nest to a nearby cottonwood. A third bird was calling but could not be clearly seen. The nest was about 35 to 40 feet above ground in the branches of a cottonwood.

In 1972, a pair built a new nest near the old site. The hawks were seen by Charles L. Hyder on 21 April 1972 near the new nest, and Brother Edwin Mattingly and I found an adult at the nest feeding young on 3 June. The second adult was nearby. Dr. Hyder obtained photographs of one of the adult birds and of the nest in April. The nesting area was checked frequently during 1973, and a single adult was seen 20 June, but no evidence of nesting was found. A Great Horned Owl (*Bubo virginianus*) did successfully raise its brood in the abandoned 1971 nest.

The known breeding range of the Black Hawk in New Mexico is generally confined to the southwestern part of the state, with reliable records as far north as the Gila Cliff Dwellings (Hubbard, op. cit.:23). There are earlier, undetailed reports of nesting along the nearby San Francisco and Mimbres rivers, plus a vague indication of occurrence in the lowermost Rio Grande Valley (Ligon, New Mexico birds and where to find them. Univ. New Mexico Press, Albuquerque, 1961:72). The breeding of this species at Alameda represents a northward extension of some 160 miles in New Mexico, notable in a hawk that is generally considered of lowland, neotropical affinity.

Tree Swallow (*Iridoprocne bicolor*).—At Elephant Butte Marsh, Sierra County, about 55 miles south of Socorro, New Mexico, I saw a pair of Tree Swallows entering and leaving a nest hole in a willow snag about seven feet above water 17 June 1972. The nest site had been used earlier in the season by a pair of Ladder-backed Woodpeckers (*Dendrocopos scalaris*). On 24 May 1973, a pair of Tree Swallows again used the nest hole. The nest, well-lined with feathers, contained one egg. Rising water, however, apparently caused failure.

This is among the southernmost breeding records for this species in New Mexico and apparently in North America. The species has been recorded previously nesting 45 miles to the north in the state, at Bosque del Apache National Wildlife Refuge, Socorro County (Ligon, op. cit.:191). The Tree Swallow also appears to have extended its range southward in the westernmost part of the state. Hubbard (Nemouria, No. 2, 1971) found a pair nesting near Cliff on 27 June 1968 and obtained photographs of the nest and eggs.

Black-capped Chickadee (*Parus atricapillus*).—On 14 June 1973, I found a family of two adults and at least three young in woodland along the Rio Grande near Alameda

(see above). The adults were feeding the young out of the nest in low brush. The young also appeared to be gleaning food on their own, although they were very recently fledged. I observed the family group for about 10 to 15 minutes from a distance of 15 feet or less.

The Black-capped Chickadee has previously been reported breeding in three northern counties of New Mexico (Hubbard, 1970:60). The southernmost breeding record to date is for the Santa Fe area, Santa Fe County (Ligon, op. cit.:207), some 45 miles northeast of Alameda. The species winters irregularly in Bernalillo County, but has not previously been known to breed so far south in the Rio Grande Valley. This appears to be the southernmost breeding record of the species in North America.

Catbird (*Dumetella carolinensis*).—I found an adult Catbird incubating four eggs in a nest in a Russian olive tree near Alameda (see above) on 30 May 1973. There were at least four additional territorial males singing in the area. The nest was about six feet above ground in an area of dense vegetation. Three young were in the nest on 10 June, along with one unhatched egg. By 14 June, the three young had well-developed feather sheathes, and on 20 June only the unhatched egg remained in the nest.

Dumetella carolinensis has been previously recorded breeding in four northern counties of the state (Hubbard, op. cit.:65). The southernmost breeding records to date are near Santa Fe and near Pecos, San Miguel County. There are also a few summer records in southwestern New Mexico in Catron County, and the species breeds in adjacent Arizona (Phillips, Marshall, and Monson. The birds of Arizona, University Arizona Press, Tucson, 1964).

I thank John P. Hubbard for his encouragement and help with this paper. I am also indebted to Barbara Escher and Charles Hyder for help with the field work.—CHARLES A. HUNDERTMARK, 506½ Sycamore SE, Albuquerque, New Mexico 87106. Accepted 4 April 1974.

THE PRESIDENT'S PAGE

MARGARET MORSE NICE,

1883-1974

On 26 June 1974, Margaret Morse Nice died at her home in Chicago, Illinois, at the age of ninety.

Mrs. Nice, in a sense, was only one of many important American contributors to ornithology in the twentieth century, but she was far more than that. She had become a symbol and an inspiration to a host of would-be ornithologists, particularly but not exclusively nonprofessionals. Dr. Mary Heimerdinger Clench, for example, tells me that it was her reading of Mrs. Nice's "The watcher at the nest" as a high school freshman that solidified her resolve to become an ornithologist. Mrs. Nice's career demonstrated to countless others that a housewife without a doctorate, raising four children, could, by studying the birds in her own backyard, make "the outstanding contribution of the present quarter century to ornithological thinking in America"—a quotation from the citation accompanying an honorary D. Sc. awarded to Mrs. Nice at her Fiftieth Reunion at Mount Holyoke College.

Mrs. Nice is survived by four daughters, seven grandsons, four great-grandchildren, a sister, and two brothers, to one of whom, Edward S. Morse of South Londonderry, Vermont, I am indebted for some of the biographical material used here. Her husband, Professor Leonard Blaine Nice, died in January 1974.

Margaret Morse Nice looms large in the history of the Wilson Ornithological Society. Her name first appears on our membership roll in 1921, and she wasted no time in adopting *The Wilson Bulletin* as a publication medium for her bird observations. The lead article in the September 1921 issue was "The roadside census" by Margaret M. Nice and L. B. Nice (her husband), then residents of Norman, Oklahoma. In the same issue's general notes is a report by Mrs. Nice on a white Cowbird. In October 1922, the Wilson Ornithological Club (as it was then called) hosted the American Ornithologists' Union meeting in Chicago. During this joint meeting a dinner was held by a group of 52 bird banders, including Mrs. Nice, who organized themselves into the still thriving Inland Bird-Banding Association.

At the 1925 meeting in Kansas City, Mrs. Nice was to have delivered her first paper at a Wilson meeting, "A study of a nesting of Magnolia Warblers," but according to the published Proceedings, she was unavoidably absent and was unable to present the paper. It was published in the *Bulletin* in 1926. Again in 1927, a paper on Ovenbirds was read by title at the meeting in Nashville in Mrs. Nice's absence. In the report of the Secretary for 1927 (published in 1928) appears the first evidence of Mrs. Nice's participation in Wilson Club matters other than as an author—her name appears in the list of those who had recruited a new member during 1927. Although the Nashville meeting, held in conjunction with the A.A.A.S. in December 1927, is officially recorded as the 14th Annual Meeting of the Wilson Ornithological Club, 1927 was a somewhat unusual year in that *another* meeting of the Club had already been held a month before in Cleveland, as a joint meeting with I.B.B.A. At this meeting Mrs. Nice did present a paper in person, on the nesting of a pair of Myrtle Warblers.

At the 15th Annual Meeting in Ann Arbor in 1928, the Nominating Committee presented, among others, the name of Mrs. Margaret M. Nice, Columbus, Ohio, for Councilor, to serve in 1929. The slate presented by the Committee was duly elected, and Mrs. Nice took up her first duties in the administration of the Wilson Club. She served on

the Council through 1931. At the 1934 meeting in Pittsburgh, Mrs. Nice was elected Second Vice-President of the Club and served in this office during 1935 and 1936. The custom had not yet been firmly established of two-year terms for officers, and Mrs. Nice was elevated to the presidency of the Wilson Ornithological Club after having served only one year, 1937, as First Vice-President.

The second and last year of Mrs. Nice's presidency, 1939, was also the first year of the long and memorable editor-ship of *The Wilson Bulletin* by Josselyn Van Tyne. At the same time that his name first appears as Editor, Margaret Morse Nice is listed as Associate Editor. Her duties were not specifically mentioned, but it is obvious from the frequency of the appearance of her name or initials that one of her main interests was ornithological literature. She remained on the editorial staff through 1949, but it was our sister journal *Bird-Banding* that received the major share of Mrs. Nice's skill at reading and interpreting a tremendous variety of ornithological books and papers. As Associate Editor of that journal from 1935 to 1942 and from 1946 until her death, Mrs. Nice prepared more than *three thousand* reviews and abstracts. Her fluency in German was particularly helpful in making the important literature in that language accessible to the non-linguists among us.

Mrs. Nice joined the American Ornithologists' Union in 1907 and was elected a Fellow in 1937. A full-length memorial, with a more thorough coverage of her ornithological career, will eventually appear in *The Auk*. Meanwhile, in these days of hypersensitive consciousness of the gender of scientists, it is perhaps excusable that we of the Wilson Ornithological Society take quiet pride in our long and close association with Margaret Morse Nice, the only woman to have served as President of any of the three major American ornithological societies.

Although there are no specifications as to who may qualify for the Wilson Society's Louis Agassiz Fuertes Research Grants-in-aid, in practice most of them have gone to graduate students. In 1969 a member of the Society, believing that alternative sources of funds were usually available to students, decided to initiate and to fund a grant for which college or university-affiliated individuals would *not* be eligible, in order to provide a stimulus as well as some financial assistance to "amateur" researchers. No name could better symbolize the kind of person we hoped to reach through this grant than Margaret Morse Nice, and the officers of the Wilson Society were gratified when Mrs. Nice agreed to our using her name for this purpose. The original fund that established the Margaret Morse Nice Grant-in-aid has been depleted. Gifts to the W.O.S. earmarked for this fund would constitute a highly appropriate memorial to Mrs. Nice, and might well help to encourage a potential, emulator, of any age and of either sex, of her accomplishments.
—KENNETH C. PARKES.

CORRECTION

An unfortunate printing error in the June 1974 *Bulletin* (86:181, line 40) resulted in an incorrect line displacing the proper one in The President's Page. The line should have read, "of the suggested changes: it had to be convinced, as stated in the *Supplement* itself."

ORNITHOLOGICAL NEWS

The International Commission on Zoological Nomenclature gives notice of the possible use of plenary powers by the Commission in suppression of the name *Anas punctata* Burchell, 1822. Further information on the matter may be obtained in the *Bulletin of Zoological Nomenclature*, vol. 30, part 3/4, 1974. Comments regarding this case (no. 794) should be sent in duplicate to the Secretary, c/o The British Museum (Natural History), Cromwell Road, London SW 7 5 BD, England, as soon as possible.

PACIFIC SEABIRD GROUP

This Group has been formed with the "primary function to increase the flow of information among persons interested in Pacific seabirds. . . . The Group will provide coordination and stimulation of the field activities of its members rather than initiating any field programs of its own. For the time being, at least, the Group will be primarily concerned with the west coast of North America and adjacent areas of the Pacific." At present, working committees are concerned with coordination of activities in: colony censusing, beached bird surveys and disasters, and pelagic observations and sea-watches. The Group is further active in seabird conservation and policy statements. *Pacific Seabird Group Bulletin*, Vol. 1, No. 1, was issued in January 1974. The regional reports (from Alaska to Mexico) list studies under way as follows: Alaska 19, British Columbia 22, Washington 8, Oregon 7, California 35, and Hawaii 2. Conservation policy statements are published concerning "Seabird conservation in the Gulf of California" and "Alaska oil and seabirds." A book review, sundry news items, and membership list, with research topics of the 152 charter members complete this issue. The *Bulletin* is planned to be issued semiannually (January and September) by the Secretary, George J. Divoky, U. S. Fish and Wildlife Service, 1412 Airport Way, Fairbanks, Alaska 99701.

NOTICE TO CONTRIBUTORS

Authors are reminded that all manuscripts should now be sent to Dr. Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State, Mississippi 39762. In addition, it should be noted that Dr. Robert J. Raikow will be the Review Editor for 1975.

ORNITHOLOGICAL LITERATURE

A COMPARATIVE STUDY OF THE EGG-WHITE PROTEINS OF PASSERINE BIRDS. By Charles G. Sibley. Bulletin 32, Peabody Museum of Natural History, Yale University, 1970:131 pp., 38 figs. Paper cover. Price not given. A COMPARATIVE STUDY OF THE EGG WHITE PROTEINS OF NON-PASSERINE BIRDS. By Charles G. Sibley and Jon E. Ahlquist. Bulletin 39, *ibid*, 1972:276 pp., 37 figs. Paper cover. \$7.50. Available from Publications Office, Peabody Museum of Natural History, Yale University, New Haven, Conn. 06520.—These two works bring up to date the studies that Sibley and his coworkers have made on egg-white proteins, and they provide a background into which these studies can be placed.

The first report starts with a description of the electrophoretic techniques used and the rationale for using the data so obtained in classification. Of particular value to those not familiar with the field are a discussion and a figure describing the effects of denaturation, sample concentration, polymorphism, and differences in number and mobility of proteins. These are important in attempting to evaluate the differences in the patterns presented in the main portion of the paper. This last consists of accounts of each passerine family, including a list of species examined and a discussion of how egg-white data agree or conflict with other sets of characters. The family accounts are preceded by historical reviews of the classification of the non-oscines and oscines, and followed by a discussion and summary, a bibliography, and a series of figures, most of them showing starch-gel electrophoretic patterns of sixteen species. The second report is essentially a continuation of the first, starting with a review of the principal characters used in the classification of birds and continuing with an updating of techniques and analysis of protein electrophoresis, accounts of each order, a summary, bibliography, and figures.

The scope of the work is world-wide, as it is based on the analysis of 6,600 specimens of egg-white representing 1,484 species and all but 10 passerine and seven non-passerine families of Wetmore's classification. These figures are slightly misleading, for some specimens were poor or unusable (e.g. those of the Vireolaniidae, Cyclarhidae, Galinidae, and *Regulus*): in some instances only a single species of highly diverse groups (e.g. woodcreepers, cotingas, and honey-creepers) was available.

Much of the work is summarized at the end of each paper, in lists of conclusions under the headings of "highly probable," "probable," "possible," and "improbable." Here one finds many things: long-held ideas are confirmed (e.g. "It is highly probable that the Alcedidae are closely related to the other charadriiform birds") or denied ("It is highly probable that *Opisthocomus* is a cuckoo"); recently suggested changes are supported ("It is possible that the nearest relatives of the Jacanidae are the Rostratulidae" and "that *Pterocles* is more closely allied to the other shorebirds than to the pigeons") or not ("It is probable that the New World vultures are closer to the other diurnal raptors than to the storks"); one's pet ideas may be given credence ("It is highly probable that *Aegithalos* and *Psaltriparus* are closely related to one another" and "It is possible that the loons are more closely related to the Charadriiformes than to any other living group"); new material is provided on many old controversial subjects, including the monophyly of the ratites, the relationships of the Hawaiian honey-creepers, and the finch-weaver-bird-estrildine problem; and finally many new ideas are presented, such as the possible relationships between *Parus* and *Certhia*, and of *Promerops* with the starlings.

The Australian passerine groups have long been one of the problem areas in avian systematics, and here Sibley has produced evidence suggesting several rearrangements.

Some of the "possibilities" relating to this fauna are that the Meliphagidae are composed of two subgroups; that *Acanthiza*, *Epthianura*, and *Pardalotus* are more closely related to one or another of the meliphagid groups than to the groups with which they were formerly allied; and that *Rhipidura* and *Sphenostoma* are related to each other and are not muscipids. These and numerous other possibilities raised in these studies point the way toward research in other areas, such as behavior and morphology, as well as to more refined electrophoretic approaches. They also go far in showing that the classification of the higher categories of birds based on phylogenetic relationships is an active field in which many new discoveries are yet to be made.

The two reports constitute a single work providing two major contributions. I predict that the first, the historical review of the classification of birds, with its extensive literature cited section, will become a standard reference for avian taxonomists. On the other hand, the data on egg-white proteins are part of a rapidly changing field. Indeed, the work on several groups has already been superseded by more recent papers by Sibley and his coworkers. One might well question combining the two contributions into single papers on the grounds that the relatively unchanging nature of the first might lead a reader to believe that the ideas in the second might change as little.

There is much to look forward to in the field of protein chemistry. Isoelectric focussing has already brought added resolution of electrophoretic patterns, and other kinds of proteins may yield results that can be compared with those from egg whites. Material from many other species is needed. For example, the relationships of *Aegithalos* and *Psaltriparus* cannot be resolved without a study of the proteins of *Paradoxornis* and its relatives, nor can the partitioning of the "Coerebidae" be tested with only egg-white of the type genus. There still remains the big question—what is the adaptive significance of the demonstrated differences in egg-white proteins? The answer to this would be a major breakthrough.—ROBERT W. STORER.

THE VISIBLE MIGRATION OF BIRDS AT OTTENBY, SWEDEN. Edited by Carl Edelfstam. Swedish Ornithological Association, Stockholm, 1972:360 pp., seven tables, numerous graphs, and 110 line drawings by Harald Wiberg. 95 Sw. cr. Available from the Swedish Ornithological Association, Runebergsgatan 8, S-114 29 Stockholm, Sweden.—This unusual hardback book with its attractive yellow cover is Supplement 7 of the Swedish ornithological periodical, *Vår Fågelvärld*. It is a compilation of migration data resulting from dawn-to-dusk counts of migrants during the summer and autumn from 1947 to 1956. The counts were made at the Ottenby Bird Station, located at the southern tip of the island of Öland just off the southeastern coast of Sweden.

From data gathered by a group of enthusiastic and determined ornithologists on 1,509 observation days, the book constructs as detailed a picture as possible of the southward diurnal migrations over one of northern Europe's major assembly points for migratory birds. The information on the quantity and time schedule of migration from June to October was gathered by trapping resting birds and by counting migrants during their daily passage. Although an incredible amount of migration data was amassed during the 10 year period, the book limits its coverage to the yearly, seasonal, and daily temporal changes in the volume of migration for each species. Yearly totals for 60 species of migrants are given in the form of histograms covering 10 pages. These data are further subdivided into a set of 10-day histograms spaced over an equal number of pages.

Finally, 180 pages are devoted to histograms of the daily totals for each of 90 species for each year, and each species has been rendered in a small attractive pen-and-ink sketch at the top of every second page. Brief commentaries on reverse migrations and weather influences are given, but synthesis of the data is in general very sketchy.

The volume is dedicated to Gustaf Kolthoff and his son, Kjell; they were the first to systematically take advantage of the rich possibilities for studying bird migration at the southern tip of Öland. Their work during eight autumns between 1876 and 1895 is classic. The present work might then be regarded as a sequel, but one must ask what this work achieves over that of the Kolthoffs? The answer is, regrettably, very little. The value of publishing partially processed data is questionable, and if one were to ever use these data in writing a paper, one would most certainly prefer to have the actual numerical data instead of the histograms, even though they are carefully done and seemingly exact.

As with all projects of this nature, there are occasional humorous albeit tragic events. One is mentioned on page 69 in a paragraph discussing missing observations: it seems that for 19 August 1947 the observations are incomplete, because the lighthouse keeper's cow devoured all the migration notes from 08:00 to 18:00 hours, corresponding to about half the volume of migration on that day! In addition to migration notes, I have found during the course of my studies that cows are also particularly fond of mist nets.—SIDNEY A. GAUTHREAU, JR.

A PORTFOLIO OF AUSTRALIAN BIRDS. Paintings by William T. Cooper, text by Keith Hindwood. Charles E. Tuttle Co., Rutland, Vermont and Tokyo, Japan, 1968:60 pp., 25 col. pls. \$17.50.—This is a large format picture-book of an small selection of Australia's more interesting or attractive birds. It also marks the world debut of a first-rate bird artist, William T. Cooper, a name to be remembered as future works appear.

Although I am familiar with few of these birds in life, Mr. Cooper's illustrations carry the conviction and strength of all good bird painting. While these vignettes are traditional in their basic conception, their style is original and contemporary. They are exceptionally well-drawn and well-composed, forceful, and inventive.

Mr. Cooper evidently uses a mixed transparent and opaque watercolor technique. In the darker values, he underpaints a tone and overpaints with a lighter tone for texture and form. There is a nice feeling for light and shadow, unusual in this mode of painting.

The pale, off-yellow color backing most but not all of the plates was, I suspect, laid in by the engraver; however, the reproduction is excellent throughout. There is one rather inexplicable aspect to the make-up of this volume—each plate fronts a blank page so that throughout the book one opens to unprinted double-page spreads. Use of the right-hand page would have permitted Mr. Hindwood to double the length of his text, which was obviously tailored to fit one page. Nevertheless, the accounts, brief as they are, nicely compliment the pictures. The whole production is of high quality and worth the rather high price.—DON R. ECKELBERRY.

PROCEEDINGS OF THE FIFTY-FIFTH ANNUAL MEETING

JAMES TATE, JR., SECRETARY

At the invitation of the University of Michigan Biological Station, the Michigan Audubon Society, and the Kalamazoo Nature Center, the Fifty-fifth Annual Meeting of the Wilson Ornithological Society was held at the University of Michigan Biological Station from Thursday, 6 June, through Sunday, 9 June 1974. The Council met in the Lakeside Laboratory Conference Room on Thursday evening. On Friday evening the film "Tip o' the Mitten" was presented by O. S. Pettingill, Jr., followed by a reception in the Residence Hall. Field trips on Friday and Saturday mornings were conducted to Reese's Bog, an ancient lakeshore bog noted for its abundance of bird life. The annual banquet was held in the cafeteria on Saturday, and a superlative slide-film presentation by Dr. and Mrs. W. Powell Cottrille followed in the Lakeside Laboratory. On Sunday many registrants took part in a field trip to the Kirtland's Warbler Management Area near Mio, or to Upper Michigan, visiting the Adams Trail, Birch Lakes, the Kingston Plains, and Seney National Wildlife Refuge.

The recipients of Wilson Society prizes announced at the annual meeting were as follows:

Louis Agassiz Fuertes Award: David S. Dobkin, Colorado State University—Effects of sympatry and allopatry on vocalizations of Rufous-sided and Green-tailed Towhees.

Margaret M. Nice Award: Arthur J. Wiseman, Cincinnati, Ohio—Body weight changes of the American Goldfinch.

Ernest P. Edwards Prize: Two Prizes given jointly rather than first and second prizes—Joseph R. Jehl, Breeding biology and sympatric relationships of the Stilt Sandpiper, and Storrs L. Olson—A Classification of the Rallidae.

Alexander Wilson Prize: Ralph E. Babcock, Kalamazoo, Michigan—Long-range pioneering: a mode of dispersal and range expansion.

Following the presentation of the Alexander Wilson Prize, Mr. Babcock made a thoughtful allocation of his prize. The text of a statement by Mr. Babcock follows:

I would like to express my sincere thanks to the Wilson Ornithological Society for the recognition of my paper, "Long-range pioneering: a mode of dispersal and range expansion," which was awarded the Alexander Wilson Prize for the best student paper presented at the 55th Annual Meeting held 6-9 June at the University of Michigan Biological Station, Douglas Lake, Pellston, Michigan.

At some time in our pursuit of activities, we all encounter some individual who has had great influence on our work. In recognition of the teaching, research and guidance of my major advisor, Dr. Richard Brewer, I would like to donate the prize money to the Michigan Audubon Society, to establish a research award to be given annually for the best paper, authored and published in the *Jack-Pine Warbler*, by a student. The recipient will be determined by the editorial board and the research committee of the M.A.S. The award will be entitled the BREWER RESEARCH AWARD, in recognition of his ecological and ornithological research and the guidance he has given past, present and will give to his future students.

This award to be given annually will be a sum of \$50.00.

I hope this award will stimulate students to publish research that otherwise does not get into print.

I also solicit support from the ornithological and ecological community to contribute to this fund and make the award a long-term sustaining award. Contributions can be made to the Michigan Audubon Society, 7000 N. Westnedge Ave., Kalamazoo, Michigan 49007.—RALPH E. BARCOCK

FIRST BUSINESS MEETING

The first business meeting was called to order by President Parkes at 09:30 Friday in the Lakeside Laboratory meeting hall. The minutes of the business meeting held at Chapel Hill, North Carolina were approved by the membership as published in *The Wilson Bulletin* (85:366-378, 1973). The President appointed the following temporary committees:

Alexander Wilson Prize: Abbott S. Gaunt, Chairman.

Auditing: William A. Klamm, Chairman; Ernest Hoover.

The Nominating Committee was announced as: Phillips B. Street, Chairman; Pershing B. Hofslund, Jeff Swinebroad.

The standing *Resolutions Committee*, chaired by Robert D. Burns was called upon to give a first reading to resolutions that had been submitted prior to the First Business Meeting. Chairman Burns read the following two resolutions:

WHEREAS the Wilson Ornithological Society, on 19 May 1973, in the course of its 54th Annual Meeting, held at Chapel Hill, North Carolina, adopted a Resolution urging the Bureau of Sport Fisheries and Wildlife and the Department of the Interior to adopt and implement more stringent regulations restricting the importation of exotic species of wildlife into the United States, and,

WHEREAS the Bureau of Sport Fisheries and Wildlife published in the *Federal Register*, on 20 December 1973, proposed regulations regarding the importation of injurious wildlife, which accept the biological fact that any species of wildlife is potentially harmful to the interests of human beings, to the interests of agriculture, horticulture, forestry, wildlife, or to the wildlife resources when introduced into a new environment, and

WHEREAS these regulations would reduce and more effectively regulate the importation of exotic wildlife into the United States,

THEREFORE, BE IT RESOLVED that the Wilson Ornithological Society expresses its appreciation to the Bureau of Sport Fisheries and Wildlife for proposing these regulations and expresses its support for the proposed regulations, and

BE IT FURTHER RESOLVED that the Society urges the Bureau to include in its regulations provision for the importation of wildlife, under permit and with adequate control, to be used for scientific and educational purposes.

WHEREAS the Caroni Swamp located in Trinidad is a valuable and the most accessible breeding area of the Scarlet Ibis, and

WHEREAS a liquid gas barge owned by Shell Oil (Trinidad) Limited is presently permitted to pass through Caroni Swamp, and

WHEREAS the Caroni Swamp is a bird sanctuary and an important tourist attraction for Trinidad,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society is opposed to any industrial activity in the main part of the Swamp, that is, the area between the Caroni River, the North/South Drain, the Madam Espagnol River, and the Gulf of Paria,

BE IT FURTHER RESOLVED that the Wilson Ornithological Society encourages the Government of Trinidad to declare the extremely valuable Caroni Swamp a National Park. The Secretary reported on highlights of the Council meeting of the previous evening. The 1975 meeting of the Wilson Ornithological Society will be held jointly with the Cooper Ornithological Society during the second week of June at Bozeman, Montana.

Report of the Treasurer—1973

FINANCIAL STATEMENTS

GENERAL FUNDS

Balance as shown by last report 31 December 1972 \$15,273.54

RECEIPTS

| | | |
|--|-------|-------------|
| Membership Dues | | |
| Active for 1973 | | \$ 3,682.00 |
| Active for 1974 | | 6,128.00 |
| Total Active | | \$ 9,810.00 |
| Sustaining for 1973 | | 210.00 |
| Sustaining for 1974 | | 450.00 |
| Total Sustaining | | 660.00 |
| Subscriptions to <i>The Wilson Bulletin</i> | | |
| For 1973 | | 2,376.00 |
| For 1974 | | 3,162.88 |
| Total Subscriptions | | 5,539.63 |
| Sales of back issues of <i>The Wilson Bulletin</i> | | 635.70 |
| Interest and Dividends on Savings and Investments | | |
| Income from General Endowment Fund | | 3,599.42 |
| Income from G. M. Sutton Colorplate Fund | | 390.68 |
| Total Interest and Dividends | | 3,790.10 |
| Royalties from microfilming back issues of <i>The Wilson Bulletin</i> | | |
| | | 226.98 |
| Total Receipts | | \$20,662.41 |

DISBURSEMENTS

| | | |
|--|-------|-------------|
| <i>The Wilson Bulletin</i> (Printing and Engraving) | | \$13,612.06 |
| Less contributions from authors and others | | 568.00 |
| Printing and Engraving Expense | | \$13,044.06 |
| <i>The Wilson Bulletin</i> (Additional Mail and Service) | | 379.28 |
| Editor's Expense | | 391.41 |
| President's Expense | | 103.87 |
| Review Editor's Expense | | 53.35 |
| Secretary's Expense | | 105.77 |
| Treasurer's Expense | | 327.77 |
| Committee Expense | | 39.00 |
| Annual Meeting Expense | | 199.84 |
| Transfer to Research and Grant-in-Aids | | 235.00 |
| Bank Charges | | .65 |

| | |
|---|-------------|
| International Council for Bird Protection | 30.00 |
| Miscellaneous Expense | 2.00 |
| Total Disbursements | \$14,912.00 |
| Excess of Receipts over Disbursements | \$ 5,750.41 |

GENERAL CASH FUND

| | |
|--|-------------|
| Checking Account | 10,059.15 |
| Savings Account | 10,964.80 |
| Balance in Peoples Bank, Starkville, Mississippi, 31 December 1973 | \$21,023.95 |

JOSSELYN VAN TYNE MEMORIAL LIBRARY FUND

| | |
|---|-----------|
| Balance as shown by last report, 31 December 1972 | \$ 407.20 |
|---|-----------|

RECEIPTS

| | |
|------------------------------------|--------|
| Sale of duplicates and gifts | 114.32 |
| Total Balance and Receipts | 521.52 |

DISBURSEMENTS

| | |
|--|-----------|
| Purchase of books | 215.74 |
| Balance in Peoples Bank, Starkville, Mississippi, 31 December 1973 | \$ 305.78 |

LOUIS AGASSIZ FUERTES RESEARCH FUND, MARGARET MORSE NICE FUND,
EDWARDS AND W.O.S. PAPER FUNDS

| | |
|--|-----------|
| Balance as shown by last report dated 31 December 1972 | \$ 152.00 |
|--|-----------|

RECEIPTS

| | |
|----------------------------------|-----------|
| Contributions | 408.00 |
| Transfer from General Fund | 235.00 |
| Total | \$ 795.00 |

DISBURSEMENTS

| | |
|--|-----------|
| Grant-in-aid | |
| To Robert C. Eckhardt | \$ 200.00 |
| To Richard L. Glinksi | 100.00 |
| To Ralph W. Schreiber and Robert W. Risebrough | 150.00 |
| To Russell P. Balda, Gary C. Bateman, and Gene F. Foster | 50.00 |
| To C. John Ralph | 100.00 |
| Total | 600.00 |
| Balance in Peoples Bank, Starkville, Mississippi, 31 December 1973 | \$ 195.00 |

AARON MOORE BAGG STUDENT MEMBERSHIP AWARD FUND

RECEIPTS

| | |
|--|-----------|
| Contributions | \$ 200.00 |
| Balance in Peoples Bank, Starkville, Mississippi, 31 December 1973 | \$ 200.00 |

SPECIAL FUND ACCOUNT

Balance as shown by last report 31 December 1972 ... 244.50

RECEIPTS

| | | |
|-----------------------------|---------------|--------|
| Prepaid Students Dues | \$ 0.00 | |
| Advanced Renewals | 208.75 | |
| Discount Due Agencies | 0.00 | |
| Total Receipts | <u>208.75</u> | |
| Total | | 453.25 |

DISBURSEMENTS 100.00

Balance in Peoples Bank, Starkville, Mississippi, 31 December 1973 \$ 353.25

ENDOWMENT FUND, GENERAL ENDOWMENT FUND

Balance in Endowment Savings Account as shown by last report,

31 December 1972 \$14,972.50

RECEIPTS

Life Membership Payments 1,812.50

Balance in Endowment Savings Account, Peoples Bank, Starkville,

Mississippi, 31 December 1973 16,785.00

Investments held as of 31 December 1973

| | |
|--------------------------------------|--------------|
| United States Government bonds | \$ 4,890.50 |
| Canadian Provincial bonds | 4,162.50 |
| Corporate bonds | 8,550.00 |
| Convertible corporate bonds | 2,775.00 |
| Convertible preferred bonds | 11,277.50 |
| Common stocks | 47,866.38 |
| Investment trusts | 7,583.00 |
| Uninvested principal | <u>10.00</u> |

Total Investments \$ 87,114.88

Total General Endowment Fund, 31 December 1973 \$103,899.88

GEORGE MIKSCII SUTTON COLORPLATE FUND

RECEIPTS

Contributions 20,000.00

Investments held as of 31 December 1973

| | |
|------------------------------------|-----------------|
| Canadian Provincial bonds | \$ 5,112.50 |
| Equipment Trust Certificates | 9,675.00 |
| Common Stocks | 3,200.00 |
| Uninvested principal | <u>1,569.85</u> |

Total Investments 19,557.35

Total, Combined Wilson Ornithological Society Endowment Funds,

31 December 1973 \$123,457.23

Respectfully submitted,
JEROME A. JACKSON, *Treasurer*

Report of the Secretary—1973

Immediately following the 1973 Annual Meeting the Secretary prepared the Proceedings for publication in *The Wilson Bulletin*. They appeared in Volume 85(3):366-378.

At the recommendation of the President I looked into the state of the Secretary's records and searched files at Cornell University and the University of Nebraska for possible archival materials. I was able to assemble a nearly complete set of minutes of Council meetings. A number of files would be suitable for inclusion in archives, and additional files will probably turn up with further checking. Before contacting past officers and others for possible inclusion in an official archive, I felt that we must settle the question of a repository first. Cornell University's Departments of Archives and Regional History seemed a reasonable place to inquire because of their large existing ornithological collections. They were not interested in more than the bare minimal files to reflect the History of the Society. The University of Michigan, due to its function as permanent address for the Wilson Ornithological Society and its retention of the W.O.S. library may well be interested. I would like to ask the wisdom of the Council on this point before proceeding to gather further potential material for archives.

The announcement, program and abstracts were prepared from material provided by local Chairman H. Lewis Batts, Jr. and Second Vice-president D. A. James. They were then edited, printed, and delivered by the secretary.

The Secretary encountered unusual delays in delivery of envelopes addressed to the membership from Allen Press, which holds our addressograph list. As a result the announcement did not reach some members until close to the deadline for papers. A full program of papers was easily obtained by the Second Vice-President however.—JAMES TATE, JR., *Secretary*

Report of the Editor—1973

Since becoming editor in June 1973, I have received 194 manuscripts, not counting book reviews, notes and news, and the President's Page. Some of the 194 manuscripts were revisions initially received under the previous editor, but the bulk was new. As of the date of this report, the fate of the manuscripts has been as follows: published 48; in press 37; accepted 5; out for refereeing 23; returned for revision 47; rejected 34.

On a volume-by-volume basis, the following is the status of Vol. 86:

- No. 1, March: 96 pp., 8 papers, 18 notes, 5 book reviews, 1 color plate; issued on 21 March 1974.
- No. 2, June: 100 pp., 10 papers, 12 notes, 9 book reviews, 1 color plate; issued on 8 May 1974 (early issue date to circulate Bulletin before the annual meeting).
- No. 3, September: pp. unknown, 16 papers, 12 notes, and several reviews (not all of this material will be used), 1 color plate (Madagascar Crested Ibis); in press and expected on time.
- No. 4, December: pp. unknown, so far 2 papers and 3 notes accepted, but will include some holdover material from September galleys, 1 color plate (2 new species of tanager) expected to be on time.

Additional color plates received and to be processed:

- Hybrid *Passerina* buntings (paper by Emlen, Rising, and Thompson for 1975)
- Edithornis* rail (paper by Storrs Olson for 1975)

Processing time was calculated, from time of receipt of any original manuscript (including those revised under previous editor) to acceptance:

44 papers published (Mar., June) or in press (Sept.)—110½ days S. D. 79½ days
46 notes (same specifications)—70 days S. D. 65 days

Based on 3½ months press time, the lead time can be put at about 7 months for a paper and just under 6 months for a note in Volume 86.

Part of the successful stream-lining in manuscript processing has been the introduction of a broader spectrum of forms, including one for referees. Referees are urged to return papers within one month and notes within one week, and to encourage this I have enclosed a self-addressed (to the editor) envelope with the manuscript. In addition, I acknowledge receipt of manuscripts returned by referees, both to express appreciation and to assure them of their safe arrival. Referees processed manuscripts at the following rates (March–September material): papers 23 days S. D. 20 days, notes 13½ days S. D. 13 days.

Needless to say, I am most gratified at this response, and a list of referees will be published in the December issue, along with my expressed thanks.

Several changes were made in the layout of the *Bulletin* for 1974. These include:

1. Elimination of the address of the editor's institution on the front outside cover.
2. Moving of the Table of Contents to the outside back cover, thus allowing us to avoid wasting this page when a year's issues were bound.
3. Moving the masthead to the top of the first page in each issue, a change necessitated by the removal of the Table of Contents to the back cover.
4. Placement of the date of acceptance of each paper and note.

In addition, I informally dissolved the Editorial Board, although I continued to use the services of its former members.

In closing, I express my appreciation to the authors, referees, Allen Press, Len Beach Associates, Peter Stettenheim (review editor), William Lunk (color plate editor), David Niles (index editor), and the many others who helped me as editor of *The Wilson Bulletin*.—JOHN P. HUBBARD, Editor

The President reported the confirmation by the Council of Jerome A. Jackson as new editor of *The Wilson Bulletin*. Reports of several of the committees which reported to the Council Meeting were then summarized. Abbreviated versions of these reports appear here.

Report of the Research Committee—1973

Your committee recommends that the Fuytes Award go to Mr. David S. Dobkin, Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80521. The title of his research project is "Effects of sympatry and allopatry on vocalizations of Rufous-sided and Green-tailed Towhees." Mr. Dobkin ranked well ahead of all but one other applicant for the Fuytes Award. The other candidate, Mr. Mike Mossman, withdrew his application on 20 May 1974, because he received sufficient financial support from other sources. There were four other strong proposals, but none of these ranked sufficiently above the others to be recommended for a second award. Nineteen people completed the application process, i.e., did more than write letters of inquiry or request forms; one of these, as noted above, later withdrew his name when he received

other support. Very few people who wrote letters indicating interest in applying did not do so.

For the Nice Award the committee recommends Mr. Arthur J. Wiseman of 2073 Hanison Avenue, Cincinnati, Ohio 45214. The title of his research project is "Body weight changes of the American Goldfinch." Only two applicants qualified for the Nice Award, and one of these was a borderline student. As often stated by Nolan in previous years, this award needs to be advertised more broadly. It is perhaps worth considering the possibility of putting undergraduates into the category of the Nice Award, as well as people not affiliated with a college or university. Undergraduates tend to have few institutional monies available to them and, in terms of quality and professional polish, their applications do not compete very well with those of graduate students. In the past years the number one candidate was always a well-advanced graduate student.—FRANK B. GILL, *Chairman*

Report of the Membership Committee—1973

Following Norman Ford's retirement as Chairman of the Membership Committee, I agreed to President Parkes' request that I take over those duties. One of my first activities was to try to determine what might be the duties of the Membership Committee, for it occurred to me that the Committee might have functions beyond a simple recruitment of new members. A review of past reports indicated that one such function might be the maintenance of membership. Accordingly I wrote to each member of the Committee, requesting that they remain for the coming year and polling their views with regard to possible functions of the Committee. Responses were received from several Committee members, and a summary of their ideas has been compiled and presented to President Parkes.

I have retained on the Membership Committee all those who responded positively to my inquiries or who have continued to contribute new members. The present Membership Committee is composed of 20 members, located in 14 states and Ontario, with the heaviest representation in the Middle Atlantic states. I am now in the process of recruiting additional Committee members to give us representation in New England (which was a surprisingly large gap in our coverage) and additional representation in the Midwest.

In addition to the individuals who responded to my initial circular, several members of the old Committee have continued to be active. Among these is Mrs. John Lueshen, who deserves special commendation for once again being the leading individual recruiter (8) on the Committee.

The Membership ad placed in the Sept. 1973 issue of *The Wilson Bulletin* has proven effective. Doug James received a number of applications that he forwarded to me. Each of those nominees then received a letter, an application form, and a pamphlet about the Society. To date we have had positive responses from 14 (about 10 percent of our new members) of these individuals. I would, therefore, recommend that such an ad be run on an annual basis, but that one change be made. Namely, that the ad be clearly divided into a student and non-student section with the addresses of both the Student Membership Committee and regular Membership Committee chairmen appropriately affixed. This should save considerable cross-mailing.

As of 13 May the Society has recruited a total of 163 new members. During the year 1973-74 we also lost 121 members, through death (8), resignation, suspension, or lack of forwarding addresses. This gives us a net gain of 42 members. Thus, for the second consecutive year we have gained more members than we lost. The new members represent 41 states, 3 Canadian provinces, and 4 foreign countries (one represented by a

Peace Corps member). Twenty-three new members were recommended by 11 members of the Membership Committee, 15 by Doug James, and 70 by the Treasurer, Jerry Jackson. The rest were recommended by 45 members of the Society, some of them past members of the Membership Committee.

Utilizing the information provided on the back of the application cards, I have attempted to compile some sort of a profile of "the new member." It must be noted that not all of the cards were filled out, and the profile may be somewhat biased. However, within those limitations, the typical new member is male (145 vs 28), has at least a bachelor's degree (82 of 108), but continues as a student (59). He was born between 1946 and 1955 (62 of 109). If he is not a student, he is a professional biologist (20) and/or is employed by an educational institution (21). It is difficult to ascertain the true interests of many recruits, as the categories listed on the back of the application card tend to bias the data. It should be noted, however, that 45 individuals expressed an interest in photography, 45 in life histories, 38 in conservation, and 34 in bird banding. A number of other individuals also wrote in various other interests, many of them related to more specialized aspects of field studies. What is perhaps of interest to the Society is that, with the possible exception of behavior (21), only one individual indicated an interest in any of the experimental or laboratory aspects of ornithology (anatomy and physiology). Either such people are extremely rare, they are not joining The Wilson Society, or the special interests listed on the card tended to direct responses away from those areas. This profile, then, strongly fits the image projected in President Parkes' recent discussion of his views of the Society in the President's Page (*The Wilson Bulletin*, September, 1973).—A. S. GAUNT, *Chairman*

Report of the Student Membership Committee—1973

In contrast to the other years since 1970, this past year was a relative success for the Committee, but it still far from equalled the number of potential new student members contacted in the banner year of 1970.

Noting the dismal failure of the annual notice in *The Wilson Bulletin* in stimulating the nomination of new student members (there were only two or three responses a year), I made a recommendation at the Council meeting in Chapel Hill last year that I felt might improve matters. I suggested that a form for nominating student members be included in the annual mailing requesting dues payment, emphasizing that the only time there was a good response to a request for student nominations was when members were contacted directly. After some discussion it was decided instead to print my form, which also asked for non-student nominations, in the September 1973 issue of *The Wilson Bulletin*. This was innovative and 16 responses produced 28 student nominations. These nominees were sent invitations to join the Society by the Student Membership Committee. We do not know how many actually elected to join, but nevertheless the number of nominations was greater than received in the immediately preceding years.

By contrast, the direct mailing in 1970 to the 429 members then associated with educational institutions produced 188 student nominations from 55 responses of which 40 nominees accepted the invitation to join the Society. Thus, I conclude that although the published membership form is very helpful, it still would be worthwhile to have a direct mailing requesting student nominations. For the sake of economy it would be best to include the form with the annual dues notice.

In addition, the Committee processed seven student nominations from other sources. Some of these no doubt were stimulated by the published nomination form.

The committee continued its annual practice of contacting natural history organizations, nature centers, and other science-oriented public institutions around the country, asking for nominations of promising pre-college students who exhibit a special interest in natural history and bird study. This year 47 mailings to 9 western states produced no responses. Last year the responses from the states in the Southeast and Great Plains had just begun to arrive by the time of the Chapel Hill meeting. We can now report that there was a total of 12 such nominations received. (This effort proceeds year by year on a region by region basis.)—DOUGLAS JAMES, *Chairman*

Report of the Conservation Committee—1973

Following the pattern established in 1971, the Conservation Committee addressed itself to specific problems suggested to the Committee through the President. The work of the Committee for 1973 consisted of two timely and important reports to be published in their entirety in future issues of *The Wilson Bulletin*. The reports are entitled "Report on the status of Sandhill Cranes," and "Report on eagles."

Lists of new members were posted in the meeting hall by the Secretary. There being no further business, the President closed the first business meeting at 09:54.

SECOND BUSINESS MEETING

President Parkes called the meeting to order at 14:40 on Saturday. The Auditor's Report was given and is reproduced here.

Report of the Auditor—1973

We are pleased to tell you that the report of the Treasurer, the books of records, and the financial statements of the banks have been examined and reconciled satisfactorily for the close of 31 May 1974.—WILLIAM A. KLAMM, *Chairman of Auditing Committee*

Robert D. Burns, Chairman of the *Resolutions Committee* read the two resolutions offered earlier, and both were passed by the membership. In addition, the following resolution was presented.

WHEREAS the Wilson Ornithological Society has held its fifty-fifth annual meeting at the University of Michigan Biological Station on Douglas Lake in northern Michigan, from 6 through 9 June 1974, and

WHEREAS the members have received much knowledge, fellowship, inspiration, and new dedication from the efforts of the Local Committee on Arrangements chaired by H. Lewis Batts, by the Michigan Audubon Society, Kalamazoo Nature Center and the University of Michigan Biological Station,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society expresses its most sincere appreciation to the sponsoring organizations and to the extraordinarily efficient local committee on arrangements for a most memorable meeting.

BE IT FURTHER RESOLVED that the Society's special thanks are due to David Gates, director of the Biological Station; William L. Foster, Olin Sewall Pettingill and H. Lewis Batts.

This resolution was accepted by the membership. The list of new members was accepted and voted into membership.

Phillips Street, Chairman of the *Nominations Committee* proposed the following slate of officers: For President, Kenneth C. Parkes; First Vice-President, Andrew J. Berger; Second Vice-President, Douglas A. James; Secretary, James Tate, Jr.; Treasurer, Ernest Hoover; Elective Member of the Council (three years), Helmut C. Mueller. There be-

ing no further nominations, the nominations were closed. A unanimous ballot was cast for the proposed slate.

The President closed the second business meeting at 15:04.

PAPERS SESSIONS

- Gustav A. Swanson, Colorado State University, Fort Collins, Colorado, *Management for Songbirds on a Retired Farm in Upstate New York*
- William G. George, Department of Zoology, Southern Illinois University, Carbondale, Illinois, *Domestic Cat Predation on Birds during Seven Consecutive Nesting Seasons in an Agro-Wildlife Habitat.*
- Harry M. Ohlendorf, Erwin E. Klass, and T. Earl Kaiser, Patuxent Wildlife Research Center, Laurel, Maryland, *Organochlorine Residues in Black-crowned Night Heron Eggs*
- S. C. Kendeigh, University of Illinois, Champaign, Illinois, *Bioenergetic Control of Latitudinal Distribution in the House Sparrow.*
- Barbara A. Lensing and Thane S. Robinson, Department of Biology, University of Louisville, Louisville, Kentucky, *Preliminary Observations of Barn Swallow Energetics.*
- Dennis M. Forsythe, Department of Biology, The Citadel, Charleston, South Carolina, and Department of Zoology, Clemson University, Clemson, South Carolina, *Individual and Geographic Variation in the Advertising Song of Indigo Buntings.*
- Robert W. Storer, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, *Sunbathing in Grebes.*
- Debbie Good, Bird Populations Institute, Division of Biology, Kansas State University, Manhattan, Kansas, *Morphological Variation, Search-Pursuit Strategies, Degree of Specialization, and the Evolution of Morphological Variation.*
- Harold F. Mayfield, Waterville, Ohio, *Kirtland's Warbler and Its Preservation.*
- Nicholas L. Cuthbert, Central Michigan University, *Kirtland's Warbler Reproductive Success with Cowbird Control in Sample Areas.*
- William F. Shake, U.S. Bureau of Sport Fisheries and Wildlife, Lansing, Michigan, *Cowbird Control on Kirtland's Warbler Nesting Areas.*
- Lawrence H. Walkinshaw, Muskegon, Michigan, *Survival of Kirtland's Warblers from Eggs Laid before and after Cowbird Removal in Crawford County, Michigan.*
- Robert B. Payne, University of Michigan Museum of Zoology, *How Many Eggs Do Brown-headed Cowbirds Lay?*
- Warren P. Faust, Ann Arbor, Michigan, *Are the Kirtland's Warblers of Crawford, Oscoda, and Ogemaw Counties Members of a Single Freely Interbreeding Population?*
- Daniel S. McGeen, Pontiac, Michigan, *The Kirtland's Warbler and Population Theory.*
- Lawrence H. Walkinshaw and Ronald Hoffman, Muskegon, Michigan, *Southern Michigan Sandhill Crane, Increase and Spread.*
- Ronald A. Ryder, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado, *Distribution, Status and Movements of White-faced and Glossy Ibises Nesting in the United States.*
- Harvey I. Fisher, Department of Zoology, Southern Illinois University, Carbondale, Illinois, *Longevity of the Laysan Albatross, Diomedea immutabilis.*
- Clait E. Braun, Colorado Division of Wildlife, Fort Collins, Colorado, *Investigations of Band-tailed Pigeons in Mexico.*
- Ralph E. Babcock, Department of Biology, Western Michigan University, Kalamazoo, Michigan, *Long Range Pioneering: A Mode of Dispersal and Range Expansion.*

- James W. Patus and Jose A. Rivera, P. R. Nuclear Center, Radioecology Division, Mayaguez, Puerto Rico, *Environmental Baseline Studies of the Avifauna of Jobos Bay, Puerto Rico*.
- Wayne C. Weber, Biology Department, Capilano College, Vancouver, British Columbia, Canada, *Urban Bird Populations in Vancouver, Canada*.
- George A. Hall, West Virginia University, Morgantown, West Virginia, *A Twenty-five Year Population Study of an Appalachian Spruce Forest*.
- John L. Zimmerman and John L. Tatschl, Division of Biology, Kansas State University, Manhattan, Kansas, *Floodplain Succession and Intraspecific Mensural Variation*.
- Richard Brewer and Keith G. Harrison, Department of Biology, Western Michigan University, *When Does Habitat Selection by Birds Occur?*
- Richard S. Boswell and Elden W. Martin, Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio, *Reproductive Success of Great Horned Owls in Northern Ohio*.
- William J. Francis, Ohio Field Station, Patuxent Wildlife Research Center, U.S. Bureau of Sport Fisheries and Wildlife, Sandusky, Ohio, *Clutch Size and Nesting Success in Red-winged Blackbirds*.
- Larry C. Holcomb, Department of Biology, Creighton University, Omaha, Nebraska, *Pituitary Prolactin in Red-winged Blackbird Females in Pre-breeding*.
- Charles M. Weise, Zoology Department, University of Wisconsin—Milwaukee, Milwaukee, Wisconsin, *Population Dynamics of the Black-capped Chickadee in Southern Wisconsin*.
- Dennis P. Duika, Ralph E. Babcock, Keith G. Harrison, and Stephen Miller, Dept. of Biology, Western Michigan University, Kalamazoo, Michigan, *Interspecific Dominance Relationships at Southwestern Michigan Winter Bird Feeders*.
- Ralph W. Dexter, Kent State University, Kent, Ohio, *Change of Prospective Mates, Replacement, Sharing and Shifting of Mates in a Nesting Colony of Chimney Swifts*.
- Jean H. Schulenberg, Admire, Kansas, and Thomas G. Shane, Junction City, Kansas, *Tree and Harris' Sparrow Associations*.
- Stephen Fretwell, Bird Populations Institute, Division of Biology, Kansas State University, Manhattan, Kansas, *Population Regulation in the Dickcissel*.
- Arlo Raim, Section of Wildlife Research, Illinois Natural History Survey, Urbana, Illinois, *Territory Shifting of Bobolinks on a Michigan Grassland*.
- Daniel E. Bowen, Bird Populations Institute, Division of Biology, Kansas State University, Manhattan, Kansas, *Nest Site Selection in a Prairie Community*.

ATTENDANCE

- From COLORADO: *Fort Collins*, Clait Braun, R. Ryder, Gustav Swanson; *Littleton*, James Tate, Jr., D. Jean Tate.
- From CONNECTICUT: *Wallingford*, Karl Tolonen.
- From WASHINGTON, D.C.: Douglas James.
- From FLORIDA: *Daytona Beach*, Mr. and Mrs. Ralph Branch; *Winter Haven*, Peggy Macqueen.
- From HAWAII: *Honolulu*, Andrew Berger.
- From ILLINOIS: *Carbondale*, Mr. and Mrs. Harvey Fisher, Mr. and Mrs. William George; *Champaign*, Mr. and Mrs. S. Kendeigh; *Chicago*, Arlo Raim; *Colchester*, Mr. and Mrs. Edwin Frank; *DeKalb*, Mr. and Mrs. W. Lory and Edith Reid, William Southern.

- From INDIANA: *Anderson*, Mr. and Mrs. John Goodman and Robert Hignell; *Bloomington*, Mr. and Mrs. Robert Johnson; *Lafayette*, Mrs. S. McSorley; *Terre Haute*, Mr. and Mrs. James Mason; *West Lafayette*, Edward Hopkins.
- From IOWA: *Cedar Rapids*, Mr. and Mrs. Robert Vance.
- From KANSAS: *Manhattan*, John Zimmerman, Dan Bowen, Phil Elliot, Stephen Fretwell, Debbie Good, Tom Shane, John Tatschl.
- From KENTUCKY: *Anchorage*, Mr. and Mrs. Burt Monroe; *Louisville*, Barbara Lensing, Mr. and Mrs. Thane Robinson.
- From MARYLAND: *Chesterton*, Mrs. Edward Mendinhall; *Laurel*, Harry Ohlendorf, Mr. and Mrs. Chandler Robbins, Jay Sheppard; *Wheaton*, Mr. and Mrs. John Willoughby, *Columbia*, Mrs. James Plymire.
- From MASSACHUSETTS: *Manomet*, Mr. and Mrs. Paul Anderson; *Petersham*, Mr. and Mrs. John Fiske.
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THE WILSON BULLETIN

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TWO NEW SPECIES FROM PERU

(above) RUFUS-BROWED HEMISPINGUS, *Hemispingus rufosuperciliaris*

(below) GOLDEN-BACKED MOUNTAIN-TANAGER, *Buthraupis aureodorsalis*

From a watercolor painting by John P. O'Neill (1/2 X)

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TWO NEW SPECIES OF TANAGER FROM PERU

EMMET R. BLAKE AND PETER HOCKING

The diversity of birdlife inhabiting the eastern slopes of the Andes and adjacent lowlands of Peru is perhaps without equal among comparable areas of the world. In recent years additional species have been recorded there with astonishing frequency through discovery both of undescribed forms and of the presence of birds not previously reported in Peru. Researchers of Louisiana State University Museum of Zoology (LSU), under the direction of George H. Lowery, Jr., have made major contributions to this new knowledge, as have those of the Field Museum of Natural History (FMNH), in continuation of the Peruvian studies that were initiated by John Todd Zimmer in 1922. Among the most recent additions to the avifauna of Peru are two colorful and strikingly distinct new tanagers (see frontispiece) collected for FMNH by the junior author and his Peruvian assistant, Manuel Villar. Specimens of both new tanagers were subsequently taken by Dr. Lowery's collectors and were made available to us for this study. In our descriptions the arc of the wing is measured, and the culmen length is from the base.

Hemispingus rufosuperciliaris sp. nov.

RUFOUS-BROWED HEMISPINGUS

HOLOTYPE.—Adult ♂ (LSU 74,727), Bosque Huaylaspampa, Depto. Huánuco, Peru, elevation approximately 8,400 ft; collected on 18 July 1973 by D. A. Tallman (original number 1524).

DIAGNOSIS.—Nearest *H. goeringi* in general appearance but appreciably larger, more richly colored below, and superciliaries uniform cinnamon-rufous rather than white.

DISTRIBUTION.—Presently known only from the temperate zone of central Peru (ca. 8,400 to 10,000 ft) in the Acomayo-Carpish Ridge region of Depto. Huánuco.

DESCRIPTION OF THE HOLOTYPE.—Top of head and nape pure black, bordered laterally by a broad cinnamon-rufous stripe that forms very prominent superciliaries; lores, orbital region, and auriculars to sides of neck black, the upperparts otherwise deep slate, darkest on the remiges (both webs) and tail; throat, breast, sides, and most of the abdomen uniform cinnamon-rufous, this replaced by dark gray slightly tinged with brown on the lower abdomen, undertail coverts, flanks, and tibiae; under surface of wings dull black.

the coverts somewhat lighter, more grayish. Iris, tarsi and toes "brown;" maxilla black; mandible blue-gray, lightest at tip. Skull ossified. Wing 72 mm; tail 65; culmen 15; tarsus 30; weight 30 g.

MEASUREMENTS.—5 ♂♂, wing 69–72 mm (mean 71.0); tail 61–67 (64.6); culmen 14–15 (14.6); tarsus 28–31 (29.2) mm. 7 ♀♀, wing 68–71 (69.8); tail 63–67 (65.0); culmen 13–15 (14.4); tarsus 28–31 (28.8) mm. Weights, 2 ♂♂ 30, 31 g (31.5); 4 ♀♀ 26–29 (27.5).

SPECIMENS EXAMINED.—Field Museum of Natural History: 2 ♂♂, 1 ♀, Huaylaspampa; 1 ♀, Torre Huasi. Louisiana State Museum of Zoology: 1 ♂, 1 ♀, Huaylaspampa; 1 ♂, Bosque Huaylaspampa; 1 ♂ (injected), 2 ♀, Bosque Cutirragra, south of Huaylaspampa; 1 ♂, 1 ♀, Bosque Magrapampa, below Zapatagocha; 1 ♀, between Zapatagocha and Huaylaspampa.

REMARKS.—The species of *Hemispingus* vary widely in color and pattern, and with few exceptions their relationships are uncertain. The new species and *H. (atropileus) calophrys* of La Paz, Bolivia, alone have rufous superciliaries: in other respects *rufosuperciliaris* appears to be more closely allied to the white-browed, gray- or grayish-backed assemblage of species with more or less strongly rufescent underparts, especially the geographically distant *H. goeringi* of northwestern Venezuela. Similarities to *H. melanotis* are much less striking, and in our opinion the relationships might best be indicated by placing *rufosuperciliaris* between *goeringi* and *verticalis* in the linear arrangement of Storer (1970).

The sexes are similar in all of the known species of *Hemispingus* and there is little individual variation in the type series of *rufosuperciliaris*. The colorful superciliaries, said to be strikingly conspicuous even in life, encroach on the black of the anterior crown in several specimens of the series, but this may be due in part to the "make" of the skin. There is also some variation in the extent of dusky coloration on the abdomen. The iris is described variously as brown, dark brown, or dark red-brown; the tarsi and toes of fresh specimens brown, grayish brown, chocolate brown, dark brown, or black. The feet of dried specimens are blackish.

Virtually all now known about the Rufous-browed Hemispingus in life is from the observations of John P. and Carol S. O'Neill, Dan A. and Erika J. Tallman, and Ronald J. Louque, all students at Louisiana State University. We are indebted to Dr. J. P. O'Neill for the following summary of combined observations, made over a period of several months in 1973.

"The new *Hemispingus* was fairly common and was seen almost every day by at least one member of the party. It inhabits the upper limits of the elfin forest but usually avoids areas where the trees are wind-stunted and mixed with grassland. It prefers places where there are thickets of ferns mixed with *Chusquea* bamboo and small bushes located near or within 'tall' elfin forest. Although occasionally seen alone, it usually travelled with groups of *Basileuterus luteoviridis* and/or *Cinnycerthia peruana*. It was never seen

more than six feet above the ground. Large groups of mixed species never contained more than two individuals of the new tanager. This contrasts with *Hemispingus atropileus*, one of the most common birds of the area, which often accompanied mixed species flocks, but travelled in groups often numbering up to a dozen individuals of that species. Within the mountain massif in which the new bird was taken, but at various elevations, we collected all other species of *Hemispingus* known to occur in Peru except the recently described *H. parodii* (Weske and Terbourgh, 1974)."

The observations of Manuel Villar, collector of six of the thirteen known specimens, differ in some details. According to Villar, this species is a forest bird that prefers the tops of the tallest trees (30–35 ft), where it searches for insects among the outermost branches and leaves, much in the manner of *H. atropileus*.

Buthraupis aureodorsalis sp. nov.

GOLDEN-BACKED MOUNTAIN-TANAGER

HOLOTYPE.—Adult ♂ (FMNH 296,538), Quilluacocha, Depto. Huánuco (Acomayo), Peru, elevation approximately 11,500 ft; collected on 2 October 1973 by Peter Hocking and Manuel Villar (original No. 1308).

DIAGNOSIS.—Similar to *Buthraupis eximia* (Andes south to Ecuador) in the deep blue coloration of crown and lesser wing coverts and in the black sides of head, throat and breast. Differs most conspicuously from all known species of the genus in having a bright, orange-yellow back and rump, elongated chestnut spots or streaks on the yellow of the abdomen and sides, and bright chestnut under-tail coverts (cinnamomeous in *eximia*) and tibiae.

DISTRIBUTION.—Confined, so far as known, to central Peru in the Acomayo-Carpish Ridge region of the Depto. Huánuco, at elevation of 10,500 to 11,500 ft.

DESCRIPTION OF THE HOLOTYPE.—Entire crown and nape deep purplish blue, approximating Cyanine or Helvetia Blue of Ridgway (1912). Throat, breast, and sides of head to upper level of eyes black, this extending to the sides of the neck and across the mantle as a broad, distinct band; back, scapulars, rump, and upper-tail coverts bright orange-yellow, with sparse, rather obscure dusky and brownish markings; lesser wing coverts blue like the crown, the wings and tail otherwise pure black; abdomen, sides and flanks bright orange-yellow like the back, the two first boldly marked with bright chestnut, elliptical spots and streaks (diminishing in size and prominence posteriorly); under-tail coverts, tibiae, and lower belly chestnut; axillaries immaculate yellow; under surface of wings black, except for a small patch of yellow on the outer edge of the carpus. Iris dark brown; bill black or blackish, lightest below; tarsus "dark gray," appearing black. Wing 126 mm; tail 95; culmen 21; width of mandible at gape 14; tarsus 36.

MEASUREMENTS.—5 ♂♂, wing 123–130 mm (mean 125.8); tail 95–102 (98.5); culmen 18–21 (19.6); width of mandible at gape 12–15 (13.2); tarsus 34–38 (36.0). 2 ♀♀, wing 121, 123; tail 94, 98; culmen 20, 22; width of mandible at gape 12, 14; tarsus 34, 36.

SPECIMENS EXAMINED.—Field Museum of Natural History: 3 ♂♂, 1 ♀, Quilluacocha, northwest of Acomayo; 2 ♂♂, Sariapunta (10,500 ft), above Llancomagon. Louisiana State University Museum of Zoology: 1 ♀, Quilluacocha.

REMARKS.—As with other species of *Buthraupis*, the sexes of *aureodorsalis* are indistinguishable. Individual variation in the type series is minimal, being reflected primarily in the relative warmth (orange infusion) of the yellow areas, and especially in the relative profusion and prominence of the chestnut ventral markings. Although nearest *eximia* in size and sharing with it several characteristics of color and plumage pattern, the striking dissimilarities of *aureodorsalis* set it apart as a distinct species. It is clearly more closely related to the assemblage of relatively large, solely montane South American species of the genus (*montana*, *eximia*, *wetmorei*) than to any of the five species that comprise the "Bangsia" complex of *Buthraupis* as revised by Storer (1970). In consideration primarily of the plumage characteristics of each, we recommend placing *aureodorsalis* tentatively between *eximia* and *wetmorei*.

The belated discovery of so large a bird of notably conspicuous plumage may indicate an extremely restricted range and specialized habitat. According to Manuel Villar, who alone is known to have observed this tanager in life, *B. aureodorsalis* is restricted to the small, scattered islands of elfin forest that dot the *pajonal* above the main forests inhabited by *B. montana*. It seems to prefer the largest leafy trees of an unidentified species with tough oval leaves about an inch long. It is said to be quiet, rather tame, and usually found in pairs.

ACKNOWLEDGMENTS

We are indebted to Dr. George H. Lowery, Jr. for the loan of comparative material under his charge and for other help. We are also deeply grateful to Dr. John P. O'Neill for providing the superb illustration of the new birds. To Dr. Antonio Brack, Sub-Director of Forestal y Caza (Conservación), Lima, we express our personal regards and appreciation for his cooperation in authorizing the field work being conducted for Field Museum of Natural History.

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TAXONOMIC STATUS OF CERTAIN CLAPPER RAILS OF SOUTHWESTERN UNITED STATES AND NORTHWESTERN MEXICO

RICHARD C. BANKS AND ROY E. TOMLINSON

This study treats Clapper Rails (*Rallus longirostris*) distributed from the Colorado Valley of Arizona and California southward along the western Mexican mainland to Nayarit. These populations have been described as belonging to three races, i.e. *yumanensis* (Colorado Valley), *rhizophorae* (Sonora and northern Sinaloa), and *nayaritensis* (southern Sinaloa and Nayarit). Our aim was to assess the validity and range of these races and to present detailed descriptions of them. In assigning the races to *R. longirostris*, rather than to the King Rail (*R. elegans*), we follow the A.O.U. Check-list (1957). We use brackets to indicate present species assignment of various forms of rails.

The U.S. Bureau of Sport Fisheries and Wildlife (1966, 1973) considers *R. l. yumanensis* to be an endangered subspecies, and for this reason Tomlinson began field studies of the birds in 1968. In making comparative studies in the Colorado River Valley and northwestern Mexico (Tomlinson and Todd, 1973), Tomlinson became concerned as to the distinctness of *yumanensis* and *rhizophorae* of Sonora. After studies had shown that the population and range of the Colorado Valley birds were greater than previously believed, in June 1971 Tomlinson collected a small series of specimens of these rails. He also took specimens from along the west coast of Mexico, south to San Blas, Nayarit. Thirty-four adults and a chick were prepared as study skins and deposited in the National Museum of Natural History (USNM). This material was augmented by previously-taken specimens, so that a total of 58 presumed breeding birds was assembled (birds in freshly molted plumage were not available). Most of the analysis was based on the strictly comparable series of 1971.

TAXONOMIC HISTORY

On 25 August 1902, Herbert Brown collected a rail that he identified as *Rallus levipes* [= *Rallus longirostris levipes*] at Yuma, Arizona. This specimen was the basis of the A.O.U. Check-list (1910) statement that *R. [longirostris] levipes* was "Accidental in Arizona." Swarth (1914) and Cooke (1914) published the basic data associated with the specimen, which is now in the collection of the University of Arizona. No other Clapper Rails were obtained in the Colorado Valley until 1921, when L. M. Huey and May Canfield took the three specimens at Bard, Imperial County, California, on

which Dickey (1923) described *Rallus yumanensis*. In a footnote, Dickey mentioned Brown's earlier Yuma specimen and indicated that it "probably" was *yumanensis*. That seems to be the last mention in the literature of that specimen, which along with Brown's use of the name *Rallus levipes* is overlooked in the essentially complete synonymies of *yumanensis* in Ridgway and Friedmann (1941) and Hellmayr and Conover (1942).

To characterize *R. yumanensis*, Dickey (1923) compared his small series with the three geographically closest forms then known, i.e. *R. [longirostris] obsoletus* and *R. [longirostris] levipes* of the Pacific Coast of the Californias and *R. longirostris saturatus* of the coastal Gulf of Mexico. The Colorado Valley birds were considered most similar to *levipes*, although separable by minor color differences of the wing coverts, alula, and underparts and by a more slender tarsus and bill. Both size and color characters were used to distinguish *yumanensis* from the two other forms, but the tabulated size differences are not impressive. Part of Dickey's (1923:93) rationale for describing the new bird as a full species was the "unique ecological niche." He remarked: ". . . it is interesting to note that we here have a true Clapper Rail inhabiting for the first recorded time a purely fresh water environment."

Huey (*in* Bent, 1926:277) believed the center of distribution of Clapper Rails in the Colorado Valley was in the delta of the river, in Sonora and Baja California; he considered the apparently sporadic northerly occurrences as stragglers driven there by flooding in the delta. Grinnell (1928) placed the Yuma Clapper Rail on the hypothetical list of birds of Baja California. In California, Moffitt (1932) reported Clapper Rails at the Salton Sea, Imperial County, and suggested that they were *yumanensis*. Abbott (1940) first referred a specimen from the Salton Sea area to this race (although specimens in the Museum of Vertebrate Zoology had been taken there in 1937) and reported several nests from which eggs had been collected.

Rallus nayaritensis was described by McLellan (1927) from a single unsexed immature bird taken at San Blas, Nayarit. This "species" was distinguished from *yumanensis*, *levipes*, *obsoletus*, *saturatus*, and *R. [longirostris] pallidus* (from Yucatan) on the basis of color and proportional size differences, the latter unsupported by any figures other than measurements of the type. This form was known only from the type until Tomlinson took specimens for the present study (*contra* Dickerman, 1971: see beyond).

Van Rossem (1929) reviewed the status of the forms *obsoletus*, *levipes*, *yumanensis*, and *beldingi* (southern Baja California) and considered them all races of *R. [longirostris] obsoletus*, a treatment followed by the A.O.U. Check-list (1931). He gave the range of *yumanensis* as "along the Colorado River, from Laguna Dam south at least to Yuma," noting that the rails of the Colorado delta were probably also *yumanensis*.

Rallus obsoletus rhizophorae was named from the area between the ranges of *yumanensis* and *nayaritensis* by Dickey (1930), who at that time also placed the latter race in *R. obsoletus*. *Rhizophorae* was said to range from Guaymas, Sonora, south to the Sinaloa border, and was described as indistinguishable from *yumanensis* ventrally but "decidedly darker and very much grayer" on the upper parts and flanks. Two color characters of the underparts were given to differentiate *rhizophorae* from the unique type of *nayaritensis*. Dickey (1930) noted that an old record for Mazatlán, Sinaloa, generally until then referred to *R. elegans tenuirostris*, should probably be referred to *nayaritensis*; however, there is no specimen to support that record (Banks, in press).

Peters (1934) recognized as subspecies *yumanensis*, *rhizophorae*, and *nayaritensis*, placing them and other western populations (the "species" *R. obsoletus*) in *R. elegans*. Oberholser (1937), who distinguished *R. elegans* from *R. longirostris*, was the first to list the three forms under consideration as subspecies of *R. longirostris*. Oberholser's arrangement and the similar treatment by Ridgway and Friedmann (1941) have been accepted generally (Friedmann et al., 1950; A.O.U., 1957), although Hellmayr and Conover (1942) followed Peters (1934). More recently, the question of species limits has been reconsidered by several workers (see Dickerman, 1971; Mayr and Short, 1970), and proposals include the lumping of all into *R. longirostris*. Regardless of the species to which allocated, *yumanensis*, *rhizophorae*, and *nayaritensis* have all been recognized as valid taxa since their descriptions first appeared.

DISTRIBUTION OF THE RACES

The breeding range of *yumanensis* has been detailed by Tomlinson and Todd (1973), and the present study confirms that birds from the delta of the Colorado River and the southern end of the Salton Sea are indistinguishable from those of the Colorado Valley. Phillips et al. (1964) have previously suggested that the race might be migratory, and Tomlinson and Todd (1973) went so far as to suggest that this form may occur within the range of *rhizophorae* in winter.

We have been able to identify migrants of this race in other areas, including two specimens from Sinaloa previously referred to *nayaritensis* by Dickerman (1971). These are from Estero Mescales, 8 km (5 mi) north of Teacapán, and Castillo, 11 km east of Mazatlán (Fig. 1). These were taken on 13 March 1935 and 17 February 1934, respectively, months that are outside the breeding season of *yumanensis* and when that race is thought to be absent from the Colorado River Valley (Tomlinson and Todd, 1973). We have also identified as *yumanensis* a specimen taken by R. W. Dickerman at Laguna San Felipe,

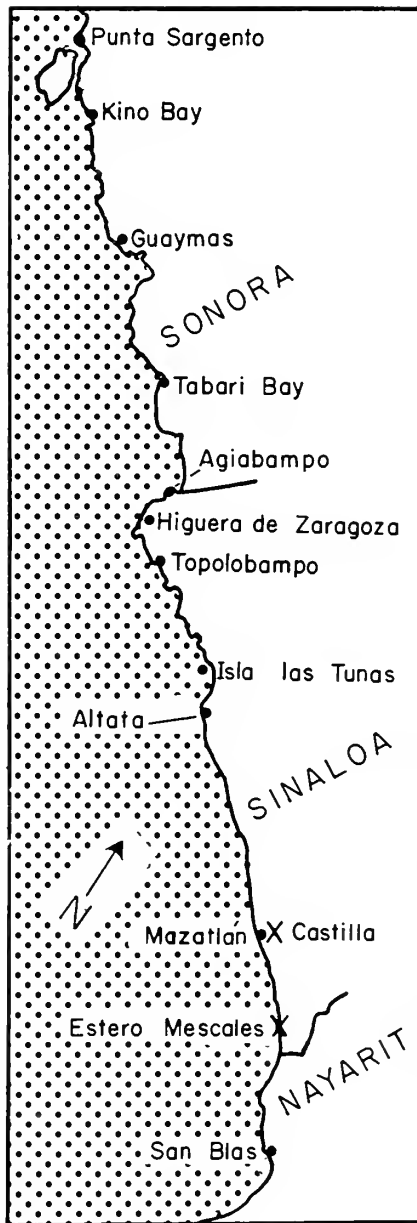


FIG. 1. Localities represented by specimens of *Rallus l. rhizophorae* and *R. l. nayariensis* used in this study and winter specimens (marked by X) identified as *R. l. yumanensis*. A map showing the breeding range of *yumanensis* may be found in Tomlinson and Todd (1973).

Puebla, Mexico, on 20 April 1962; Dickerman (1971) had referred it to the race *rhizophorae*. These three specimens, the identification of which is discussed beyond in detail, provide the first information on the wintering range of *yumanensis*.

Tomlinson and Todd (1973) also presented new data on the northern limits of *rhizophorae* in Sonora, citing specimens taken near Punta Sargento at the northern limits of mangroves. To the south, they referred specimens to this form taken at Topolobampo, Sinaloa, as did Dickerman (1971) with birds from Isla las Tunas, Sinaloa (Fig. 1). In 1971, Tomlinson collected two birds 55 km (35 mi) southwest of Culiacán, at Altata, Sinaloa. Beyond there exists a gap of approximately 140 miles (230 km), in which specimens or other records are lacking and where suitable habitat either does not exist or is scanty.

It would be convenient to consider Altata the southern limit of *rhizophorae*, except that the two specimens from there and the two from Topolobampo share color characters associated with the more southern *nayaritensis*. On the other hand, the specimens from Isla las Tunas agree, as Dickerman (1971) noted, with *rhizophorae*. Two interpretations of distributional limits may be suggested. One, the range of *rhizophorae* may reach its limits in the vicinity of Higuera de Zaragoza, Sinaloa, with a disjunct insular population on Isla las Tunas, or the area from Topolobampo to Altata could be considered one of intergradation of these races. Neither explanation is particularly satisfying, and additional specimens from this area will be needed to clarify the situation.

South of the hiatus in Sinaloa (Fig. 1) occurs *nayaritensis*, which is found in the vicinity of Mazatlán (Estero Sirena) and at San Blas, Nayarit (and presumably in suitable habitat between these points). Both *nayaritensis* and *rhizophorae* appear to be permanently resident in the areas from which breeding birds have been taken. At least we have seen no evidence of the birds being absent at any season from the area or present anywhere outside that area.

COLOR CHARACTERS

Extensive individual variation is a complicating factor in assessing Clapper Rail taxonomy. In addition, the coloration of most of the body plumage is subject to such wear, fading, and staining that detailed comparison of populations on that basis is of doubtful value. As a generality, *yumanensis* is pale and brown, *rhizophorae* is pale and grayer, and *nayaritensis* is darker and gray. Additionally, characters of the head and neck coloration exist that permit specimens of the three races to be distinguished.

In *yumanensis* the area of the lores is essentially concolorous with the

brownish-gray subocular stripe. In the few instances where the lores are darker, they are also browner. The postocular and auricular regions are pale brownish-gray. In *rhizophorae* the loreal area is usually darker than the subocular stripe, and the basic color is gray rather than brown. The postocular-auricular regions are pale gray, with little or no trend toward brownish. The lores of *nayaritensis* are much darker than the gray subocular stripe, and the entire facial area is darker than in *rhizophorae*. The color of the facial area of *nayaritensis* may also extend slightly farther onto the throat than in the other forms: however, the apparent extent of color is easily influenced by the make of the skin.

The crown and nape of *yumanensis* are brown, slightly if at all darker than the hind neck. In *rhizophorae* the crown and the nape are grayish-brown, somewhat darker than the hind neck. In *nayaritensis* the crown and nape are dark brown and contrast markedly with color of the hind neck. The sides of the neck in *yumanensis* are essentially the same color as the throat and upper breast. In both *rhizophorae* and *nayaritensis* the rufescent color of the throat does not extend as far dorsally but is more restricted to the ventral surface. This character is noticeable only when specimens are viewed from the side, and it can be masked or distorted by the make of the skin.

The similarity of *yumanensis* to *R. longirostris levipes* of coastal southern California has been stressed by several authors (Dickey, 1923; van Rossem, 1929). Compared to *levipes*, *yumanensis* is paler on the breast and throat, has grayer flanks and duller wing coverts, and is more extensively brown on the crown. Both *rhizophorae* and *nayaritensis* are grayer than *levipes*.

WING TIP CHARACTERS

Fairly constant differences in the configuration of the wing tips and in the relative length of certain primaries offer means of separating most *yumanensis* from most *rhizophorae* and *nayaritensis*. In general, *yumanensis* has a more pointed wing than do the other forms, which have the wing more rounded. This is perhaps related to the migratory nature of *yumanensis*. In *rhizophorae* and *nayaritensis*, primaries $9 = 8 = 7 = 6$ (counting from outside), or 6 is slightly shorter than the others. In *yumanensis*, $9 = 8 = 7$, with 6 noticeably shorter. To quantify this relationship, we measured the distance from the tip of the longest primary to the tips of the sixth, as well as the fifth, primaries (Table 1, Fig. 2). These distances were considerably greater in *yumanensis* than in *rhizophorae* and *nayaritensis*, although there is some overlap. Individual measurements are plotted (Fig. 2) to show that the amount of overlap is not as great as suggested by the extreme range of values.

In *yumanensis*, primary 10 (outer) is approximately equal to primary 4 in length in all 11 females and in 11 of 17 males examined (the remaining

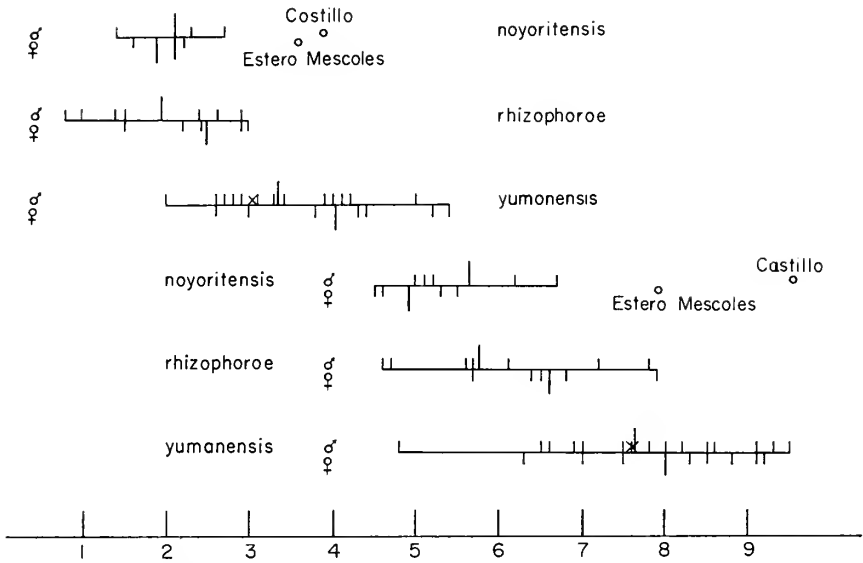


FIG. 2. Individual measurements (mm) from wing tip to end of sixth (upper set of figures) and fifth (lower set) primaries in *Rallus l. nayaritensis*, *R. l. rhizophorae*, and *R. l. yumanensis*. Two winter specimens identified as *yumanensis* in southern Sinaloa are marked by circles on the *nayaritensis* lines and another from Puebla is indicated by an X on the *yumanensis* lines.

males have primary 10 about equal to 3 in length or between 3 and 4). In *rhizophorae* and *nayaritensis*, primary 10 is relatively shorter, approximately equalling primary 3 (occasionally 2) in length, or at most being between 3 and 4. In only one male of the 28 specimens examined is primary 10 approximately equal to 4.

The Sinaloa and Puebla specimens previously mentioned as being identified as migrants of *yumanensis* were distinguished from other races primarily on the basis of wing characters. The measurements to the tips of primaries 6 and 5 of the two Sinaloa specimens are plotted (Fig. 2) with *nayaritensis*, with which they were geographically associated. Their values are far out of range of variation of the small sample of *nayaritensis* but well within the range for *yumanensis*; both have very pointed wing tips. Dickerman's (1971) identification of these birds as *nayaritensis* was based largely on color comparisons with the then unique type, which is an immature bird taken in October and of little value for such comparisons. The Puebla specimen, plotted with *yumanensis* (Fig. 2) has wingtip measurements that fall very close to the mean of measurements of that race; these are at or beyond the extremes recorded for *rhizophorae*, to which the bird was originally referred (Dicker-

TABLE 1
MEASUREMENTS (MM) FROM THE WING TIP TO THE TIPS OF PRIMARIES 6 AND 5 IN THREE
CLAPPER RAIL POPULATIONS

| | Males | | | Females | | |
|-----------|---------------------|--------------------|-------------------|---------------------|--------------------|-------------------|
| | <i>uayaritensis</i> | <i>rhizophorae</i> | <i>yumanensis</i> | <i>uayaritensis</i> | <i>rhizophorae</i> | <i>yumanensis</i> |
| PRIMARY 6 | | | | | | |
| N | 5 | 11 | 17 | 6 | 6 | 10 |
| Range | 1.4-2.7 | 0.8-2.9 | 2.0-5.0 | 1.6-2.2 | 1.5-3.0 | 2.6-5.4 |
| Mean | 2.1 | 1.9 | 3.3 | 1.9 | 2.5 | 4.0 |
| S.D. | 0.6 | 0.7 | 0.8 | 0.3 | 0.6 | 0.9 |
| PRIMARY 5 | | | | | | |
| N | 5 | 11 | 17 | 6 | 6 | 10 |
| Range | 5.0-6.7 | 4.6-7.8 | 4.8-9.5 | 4.5-5.5 | 5.7-7.9 | 6.3-9.2 |
| Mean | 5.6 | 5.7 | 7.6 | 4.9 | 6.6 | 8.0 |
| S.D. | 0.8 | 1.0 | 1.2 | 0.4 | 0.7 | 1.0 |

man, 1971). This specimen was taken at the same time and place as an example of *Rallus elegans tenuirostris* (Dickerman, 1971), the identification of which we have confirmed.

MENSURAL CHARACTERS

Oberholser (1937) and Ridgway and Friedmann (1941) presented measurements of the populations discussed here, but they had very few specimens at hand. Our measurements (Table 2) are of adult birds considered to be on the breeding grounds, with immatures and presumed migrants excluded. Although *rhizophorae* appears to average slightly larger than *yumanensis* or *uayaritensis* in most characters, the differences are slight and the overlap is nearly complete. Without resorting to statistical analysis, we would surmise that measurements do not provide a reliable criterion for separation of these forms, either inter se or from most other Clapper Rails of the western United States and Mexico. Rails of the northern population, *yumanensis*, average somewhat less in weight than those of the Mexican coastal areas, although again there is extensive overlap. Sample sizes of the Mexican forms are not large enough for firm conclusions.

SPECIMENS EXAMINED

R. l. yumanensis.—**Arizona**, YUMA CO.: Lower Topock Marsh, near Lost Lake (1, USNM); Topock Gorge, approx. 17 mi S. Needles, Calif. (3, USNM); Cibola Lake (2, USNM); Bill Williams Delta, 15 mi NE Parker Dam (1, 1 imm, USNM); Maritime Lake (1, USNM); 7 mi N Imperial Dam (1, USNM); Lake Moovalya, 7 mi N Headgate Rock

TABLE 2
MEASUREMENTS (MM) AND WEIGHTS (GM) OF THREE CLAPPER RAIL POPULATIONS

| | Males | | | Females | | |
|--------------------------------|---------------------|--------------------|-------------------|---------------------|--------------------|-------------------|
| | <i>nayaritensis</i> | <i>rhizophorae</i> | <i>yumanensis</i> | <i>nayaritensis</i> | <i>rhizophorae</i> | <i>yumanensis</i> |
| WING CHORD | | | | | | |
| N | 6 | 11 | 17 | 6 | 6 | 11 |
| Range | 143.4-155.0 | 148.6-164.1 | 143.1-160.1 | 131.3-144.6 | 135.2-146.2 | 135.6-148.5 |
| Mean | 149.9 | 152.9 | 149.8 | 139.7 | 142.3 | 141.8 |
| S.D. | 3.8 | 4.6 | 4.0 | 5.4 | 3.9 | 3.6 |
| TAIL LENGTH | | | | | | |
| N | 6 | 9 | 17 | 6 | 6 | 10 |
| Range | 62.6-66.1 | 61.5-72.8 | 60.3-69.0 | 56.7-64.1 | 55.8-66.2 | 57.8-62.6 |
| Mean | 62.8 | 65.2 | 64.2 | 60.1 | 61.7 | 59.9 |
| S.D. | 3.1 | 3.5 | 3.0 | 3.0 | 3.4 | 1.7 |
| EXPOSED CULMEN | | | | | | |
| N | 6 | 11 | 16 | 5 | 6 | 10 |
| Range | 56.4-62.5 | 58.2-64.2 | 55.4-61.8 | 54.1-59.2 | 50.7-60.4 | 51.9-58.2 |
| Mean | 59.3 | 60.4 | 59.2 | 56.8 | 56.2 | 55.5 |
| S.D. | 2.2 | 1.9 | 1.8 | 2.1 | 3.4 | 2.1 |
| TARSUS LENGTH | | | | | | |
| N | 5 | 10 | 15 | 6 | 5 | 9 |
| Range | 51.4-58.5 | 48.5-54.6 | 47.9-55.0 | 41.8-48.3 | 45.8-51.2 | 43.0-49.5 |
| Mean | 54.1 | 51.9 | 50.3 | 46.4 | 48.7 | 45.4 |
| S.D. | 2.7 | 2.0 | 2.3 | 2.3 | 2.1 | 2.0 |
| MIDDLE TOE WITHOUT CLAW | | | | | | |
| N | 6 | 11 | 16 | 6 | 6 | 10 |
| Range | 49.9-53.8 | 49.4-58.4 | 50.3-54.6 | 42.3-50.5 | 45.8-51.7 | 46.5-51.1 |
| Mean | 52.0 | 53.2 | 52.7 | 47.8 | 49.0 | 49.0 |
| S.D. | 1.5 | 2.6 | 1.3 | 2.9 | 1.9 | 1.4 |
| WEIGHT | | | | | | |
| N | 6 | 7 | 17 | 6 | 2 | 8 |
| Range | 251-305 | 261-336 | 222-307 | 210-310 | 239-268 | 192-268 |
| Mean | 280 | 297 | 256 | 267 | 253 | 219 |
| S.D. | 18.2 | 27.3 | 24.3 | 35.0 | — | 23.2 |

Dam (1, USNM); 3½ mi upriver from confluence of Gila and Colorado Rivers (1, USNM); confluence of Gila and Colorado Rivers (1, USNM); Yuma (1, 1 imm, UA). **California**, SAN BERNARDINO CO.: Headgate Rock Dam (1, USNM). IMPERIAL CO.: Palo Verde Lagoon (1, USNM); 3 mi S Cibola Lake (1, USNM); Alamo Canal, 1 mi from Morelos Dam (1, USNM); Bard (1, USNM); Alamo Duck Preserve, 8 mi NW Calipatria (7, MVZ). **Sonora**: Colorado River delta, 5 mi W Indiviso (4, USNM). **Sinaloa**: Castillo (1, MLO); Estero Mescales, 5 mi N Teacapán (1, MLO). **Puebla**: Laguna San Felipe (1, CU).

R. l. rhizophorae.—**Sonora**: Punta Sargento (1, UA); Punta Arenas (1, unsexed, UA); across from Punta Tortuga on Tiburón Island (1, UA); Long Point, 5 mi N Kino Bay (1, UA); Kino Bay estuary (2, UA); Estero Soldado, 6 mi W Guaymas (2, USNM); Tobari Bay near Paredón, 30 mi W Navojoa (2, USNM); Agiabampo (1, MLO). **Sinaloa**: Higuera de Zaragoza (3, WFVZ); Isla las Tunas (1, WFVZ; 3, MLO).

R. l. nayaritensis.—**Sinaloa**: Topolabampo (2, USNM); Altata (2, USNM); Estero Sirena, Mazatlán (3, USNM). **Nayarit**: 1 mi N San Blas (5 + 1 chick, USNM).

SUMMARY

Examination of 58 Clapper Rail specimens taken in the breeding season from the Colorado Valley and the west coast of mainland Mexico verifies the distinctness of the races *Rallus longirostris yumanensis*, *R. l. rhizophorae*, and *R. l. nayaritensis*. *Rallus l. yumanensis* is a relatively pale brown, pointed-winged, summer resident of freshwater marshes along the valley and delta of the Colorado River. Late winter specimens of *yumanensis* have been taken in freshwater and saltwater habitats in the Mexican states of Sinaloa and Puebla. Both *R. l. rhizophorae*, a pale grayish bird, and *R. l. nayaritensis*, a darker grayish form, are presumed year-round residents of the western Mexican mangrove swamps. Both have more rounded wings than *yumanensis*. The range of *rhizophorae* extends south along the coast from central Sonora to central Sinaloa, and that of *nayaritensis* from central Sinaloa to the vicinity of San Blas, Nayarit. Features of the range and characters of birds where the range of these two races approach each other are unclear.

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PREY REMAINS OF BARN OWLS IN THE SOUTHERN BAHAMA ISLANDS

DONALD W. BUDEN

Numerous reports on the feeding habits of the Barn Owl (*Tyto alba*) in the continental United States indicate that mammals, particularly rodents, are the main prey of this species and that other food items at most form a small part of its diet. Wallace (1948), for example, indicated that mammals accounted for 98.93 percent and birds 1.07 percent of the total prey items in 2,200 pellets from East Lansing, Michigan. Stupka (in Wallace, op. cit.) found that birds accounted for 1 to 2 percent of the food items at three different stations in Ohio. Baumgartner and Baumgartner (1944) found many rodent remains but no bird remains among 380 food items in pellets and skeletal debris from a site in Oklahoma. Bailey and Neidrach (1965:410) reported that the food items over a four-year period at one nesting site in Morgan County, Colorado, consisted of kangaroo rats (*Dipodomys* spp.) and several species of mice, with no bird remains in evidence. Many other similar reports could be cited.

In his report on prey species utilized by the Barn Owl on Grand Cayman in the West Indies, Johnston (1974) stated that these owls consumed a markedly higher percentage of avian prey than did their continental counterparts. He found (op. cit.; pers. comm.) that bird remains constituted approximately 40 percent of all identified bones and other food remains taken from three different sites on Grand Cayman. Most of the non-avian bones were of black rats (*Rattus rattus*) and house mice (*Mus musculus*). In addition to the bird and rodent remains, he also found skulls of the large gekkonid lizard *Aristelliger praesignis* and of two species of bats previously unrecorded from the Cayman Islands, *Brachyphylla nana* and *Artibeus jamaicensis*. Johnston theorized that the relatively high percentage of avian prey taken by Barn Owls on these small islands may be a result of the reduced diversity and numbers of potential mammalian prey. On the whole, however, there is a dearth of information regarding prey preferences of the Barn Owl in the West Indies, especially on the smaller islands.

METHODS AND STUDY AREA

From 1970 to 1972 I collected skeletal remains of small vertebrates from Recent cave sites in the Bahamas south of the Crooked Island Passage (Fig. 1). The material was found near the mouths of caves, in the form of owl pellets, or, more often, as concentrations of loose bones. The presence of pellets among assemblages of loose bones, as well as the fact that many loose bones occurred at known Barn Owl feeding sites in Johnston's (1974)

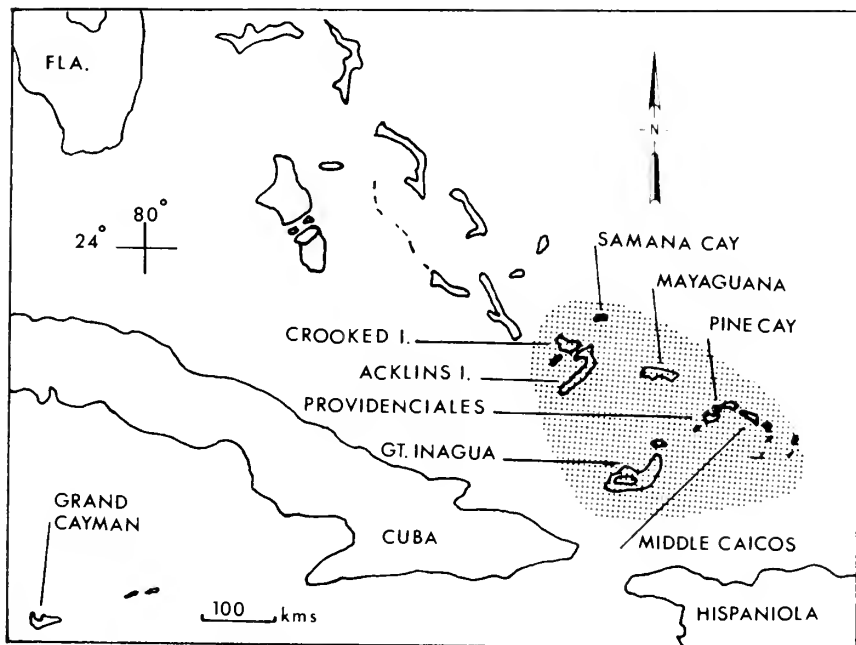


FIG. 1. Map of the Bahamas and adjacent land areas; stippling denotes the region of the southern Bahamas.

Grand Cayman study, suggest that my Bahamian samples represent food remains of owls, at least for the most part.

According to Bond (1956) two species of owls are known as residents in the southern Bahamas, the Burrowing Owl (*Speotyto cunicularia*) on Samana Cay and Great Inagua and the Barn Owl on Crooked Island and Great Inagua. Other species of owls may occur as vagrants in the southern Bahamas (for example, *Asio flammeus* on Grand Turk—Schwartz and Klinikowski, 1963), but these would probably make only negligible contributions to accumulations of prey debris left by resident owls.

Because *Speotyto cunicularia* is characteristically an inhabitant of open areas and rarely frequents caves, and because I have seen feathers of Barn Owls or the actual birds at all sites where I obtained my skeletal samples, I believe it reasonably safe to assume that all my samples pertain to Barn Owls.

The Bahamian collection sites include Crooked Island, Acklins Island, Mayaguana, and two islands on the Caicos Bank (Providenciales and Middle Caicos). Among these sites, Crooked Island is the only one where the Barn Owl has been recorded previously (Bond, op. cit.). I also observed a Barn Owl on Pine Cay (a small islet between Providenciales and North Caicos) on 23 May 1970. I was unable to locate the bird's roosting site, which, according to some of the local residents, was a "hole in the rocks" in a more remote section of the cay.

I identified skull material through reference to collections at Louisiana State University and Harvard University. The identifications are my own, but several were verified by

TABLE 1
VERTEBRATES IDENTIFIED FROM SKULL MATERIAL FROM RECENT CAVE DEPOSITS IN THE
SOUTHERN BAHAMAS (NUMBERS INDICATE INDIVIDUALS)

| | Crooked Island | Acklins Island | Mayaguana | Providenciales | Middle Caicos | Total |
|--------------------------------------|-------------------|-------------------|-----------|----------------|------------------|-------|
| RODENTS: | | | | | | |
| <i>Rattus</i> spp. | 71 | 2 | 14 | 128 | 59 | 274 |
| <i>Mus musculus</i> | | | 4 | 4 | 3 | 11 |
| BATS: | | | | | | |
| <i>Macrotus waterhousii</i> | | | | 3 | | 3 |
| <i>Artibeus jamaicensis</i> | | | | 1 | | 1 |
| <i>Lasiurus</i> sp. cf. <i>minor</i> | | | 1 | | | 1 |
| <i>Tadarida brasiliensis</i> | 2 | | | | | 2 |
| BIRDS: | | | | | | |
| <i>Porzana carolina</i> | | | | | 1 | 1 |
| <i>Charadrius wilsonia</i> | | | | 1 | | 1 |
| <i>Columbina passerina</i> | | | | 2 | | 2 |
| Columbidae spp. | | | | 4 | | 4 |
| <i>Coccyzus</i> spp. | | | | 2 | | 2 |
| <i>Tyrannus dominicensis</i> | | | | 2 | | 2 |
| <i>Margarops fuscatus</i> | 3 | | | | | 3 |
| Mimidae spp. | | | 1 | 10 | | 11 |
| <i>Vireo</i> spp. | | | 2 | 19 | 1 | 22 |
| <i>Coereba flaveola</i> | 1 | | 1 | 3 | 1 | 6 |
| Parulidae spp. | | | 1 | 1 | | 2 |
| <i>Spindalis zena</i> | | | | 2 | | 2 |
| Unidentified | | | | 4 | | 4 |
| LIZARDS: | | | | | | |
| <i>Anolis scriptus</i> | | | 3 | | | 3 |
| TOTALS | 77 | 2 | 27 | 186 | 65 | 357 |

others (see Acknowledgments). Unless otherwise indicated the nomenclature follows that of Hall and Kelson (1959) for mammals, Bond (1956) for birds, and Schwartz and Thomas (in prep.) for reptiles and amphibians. Skeletal material from the Bahamas has been deposited in the Louisiana State University Museum of Zoology (LSUMZ).

RESULTS AND REMARKS

The identification of the 357 individuals represented in my samples of skulls and skull fragments from the Bahamas is given in Table 1. The ratio of individual bird to mammal remains for each Bahamian sample is as follows: Crooked Island 4/73 (5.5 percent), Mayaguana 5/19 (26.3 percent), Providenciales 50/136 (36.8 percent), and Middle Caicos 3/62 (4.8 percent). The sample from Acklins Island consists only of skull fragments of two rats.

Although 62 is a relatively high total of bird skulls, the incidence (18.7 percent) of avian remains in my samples is much less than Johnston's figure of about 40 percent for three samples from Grand Cayman. Different yet are Barn Owl pellets reported from Hispaniola by Wetmore and Swales (1931), one sample having a bird/mammal ratio of 34/97 (35.1 percent) and the other 9/144 (6.3 percent). Even so, the incidence of bones in all these West Indian samples is higher (4.8 to ca. 40 percent) than in continental North American samples mentioned above (0 to 2 percent).

Particular skeletal items associated with Barn Owl feeding sites in the West Indies merit additional comments.

Rodents.—The 117 specimens of *Rattus* that I identified to species comprised 116 *R. rattus* and only one *R. norvegicus*. Johnston's largest sample from Grand Cayman included 30 specimens of *R. rattus* and one of *R. norvegicus*. In their study of rats in the West Indies, Schwarz and Schwarz (1965) pointed out several ecological factors that could account for the seemingly greater abundance of *R. rattus* over *R. norvegicus* on many islands in the West Indies, particularly in the southern Bahamas: 1, *norvegicus* is found on ships far less frequently than is *rattus*; 2, a relative scarcity of fresh water (as occurs on many small islands) is much more unfavorable for *norvegicus*; and 3, *norvegicus* is mostly an urban rat, whereas *rattus* is mostly a rural rat. Clearly, the small, relatively arid, and isolated islands of the southern Bahamas, with their settlements relatively small and mostly confined to the coast, and with agricultural plots scattered throughout much of the interior, seem more ideally suited for *rattus* than for *norvegicus*. I have seen presumptive *R. rattus* even on the most bleak and barren islets of the Turks and Caicos banks, where the species is able to subsist under extreme xeric conditions apparently without benefit of resources provided by humans.

Rats are clearly the dominant item in my Bahama sample (76.5 percent). Where rodents are readily available, Barn Owls sometimes subsist almost entirely on them, even in the Bahamas. For example, Northrop (1891) at a nest site on Andros Island found a large number of remains of *Rattus* but none of birds.

Bats.—Nearly all the bat bones from my Bahamian samples are of species that are presently common components of the fauna. An exception is the skull of *Lasiurus* sp. (LSUMZ 18,313) taken from a cave on Mayaguana, near the site of the former U.S. military base, on 10 May 1972. This represents a new distribution record for the genus, which has been taken previously in the Bahamas on New Providence, Andros Island, Cat Island, Long Island, Great Inagua, and the Caicos Bank (Koopman et al., 1957). Fewer than two dozen specimens of *Lasiurus* are known from the Bahamas, and their taxonomic status is open to question. Populations of *Lasiurus* in Hispaniola

and the Bahamas are currently segregated under the name *minor* and are treated either as a monotypic species (Hall and Kelson, 1959), or as a subspecies of a wide-ranging, predominantly continental species, *L. borealis* (see Koopman et al., op. cit.).

A skull of *Artibeus jamaicensis* (LSUMZ 18,309) was taken by me on Providenciales, in a cave located less than 0.5 miles (0.8 km) north of the airport at Blue Hills on 25 February 1972. I collected two other individuals of this species (preserved in alcohol) on Providenciales on 17 May 1970. These are an adult male (LSUMZ 15,633) and a gravid female (LSUMZ 15,632), bearing a fetus with a crown-rump length of 12.8 mm, taken from an undercut section of a solution hole, located near the north coast between the settlement of Blue Hills and the Third Turtle Inn. This species has not been reported previously from the Caicos Bank, but specimens have been taken in the southern Bahamas on Great Inagua and Mayaguana.

Birds.—Most of the identified bird remains in my Bahamian samples are small to medium-sized passerines. Mockingbirds (*Minus gundlachi*), thrashers (*Margarops fuscatus*), and vireos (*Vireo* spp.) are among the most common representatives. Of at least 12 avian genera found in the samples, *Vireo* provided the most specimens. I identified 22 individuals (35.5 percent of all avian items) as members of this genus. In three sets of pellets from Hispaniola, vireos made up 4.0 percent, 35.3 percent, and 17.4 percent of the identified avian prey items (Wetmore and Swales, 1931). No vireos were found by Johnston (1974) in samples from Grand Cayman, although *V. crassirostris* and *V. magister* are common there (Johnston et al., 1971).

Of particular interest among the avian remains are an incomplete skull of *Porzana carolina* (LSUMZ 75,512), taken on Middle Caicos on 29 January 1972, and two incomplete skulls of *Spindalis zena* (LSUMZ 75,513 and 75,514), taken on Providenciales on 25 February 1972. No previous records of these species from the Caicos Islands have been published, although other specimens of *P. carolina* have been taken on South Caicos (Schwartz collection: AS 1533—study skin) and Middle Caicos (LSUMZ 71,486—specimen in alcohol).

I did not see any living representatives of the tanager *Spindalis zena* during four months of field work in the Turks and Caicos Islands. The nearest islands where the species has been taken are Great Inagua and Mayaguana, each more than 30 miles (48.3 km) from the Caicos Bank. Although a small population of *Spindalis* may now occur on one or more of the Caicos Islands, a more likely possibility is that members of the genus inhabited the Caicos Islands in the past (or at least reached Providenciales at one time). Extinction rates and faunal turnover rates on small islands are notably high, especially for birds (Mayr, 1965), and the number of successful colonizations on islands

is undoubtedly less than the number of landfalls made by potential colonists (see for example Heatwole and Levins, 1973; Levins and Heatwole, 1973).

Of interest is the near absence of domestic fowl (*Gallus gallus*) bones in all the samples under discussion, in view of the fact that many West Indians maintain small flocks of chickens. Only one of four pellet sets from Hispaniola had remains of *Gallus* in it, and these amounted to only three of 34 items (Wetmore and Swales, 1931). No chicken remains were found in the Grand Cayman material (Johnston, 1974), and the species is unknown in owl prey remains anywhere in the Bahamas. This situation may perhaps be attributed more to the care that West Indians take in housing their fowl at night than to any voluntary abstinence on the part of owls.

Amphibians and reptiles.—In comparison to birds and mammals, the herpetofauna seems to play only a minor role as prey for Barn Owls. Nevertheless, loose bone and pellet samples have fairly frequently contained remains of amphibians and reptiles: *Hyla*, *Anolis*, and *Ameiva* on Hispaniola (Wetmore and Swales, 1931); the afore-mentioned specimen of *Aristelliger* on Grand Cayman; and specimens of *Anolis* on Mayaguana (my material).

For the most part, the occurrence of these herpetological remains is not surprising. Lizards of the genus *Aristelliger*, for example, often may be seen on Grand Cayman at night, crawling along the walls and roof edges of old buildings or on the trunks and larger branches of trees (pers. obs.). Anoles, on the other hand, are basically diurnal, but many characteristically sleep extended lengthwise, and exposed, on the surfaces of branches and leaves. The occurrence of a specimen of *Ameiva* is somewhat unexpected. This is a genus of diurnal, ground-dwelling lizards that are most active during the brightest and hottest part of the day. They characteristically seek shelter in underground burrows or under trash heaps toward late afternoon. One would not expect to find any "normal," healthy individuals of *Ameiva* exposed at night, when Barn Owls are usually feeding.

In the Hispaniolian remains, the abundance of *Hyla dominicensis* bones is particularly striking (Wetmore and Swales, 1931). Taking into account the relatively large size of this frog (greatest snout-vent length ca. 60 to 75 mm, fide Cochran, 1941) and its habit of resting exposed on rocks and vegetation at night, one can easily appreciate the potential of individuals of this species as prey items for Barn Owls. Furthermore, the loud frequent calls of this frog may possibly attract owls.

Interestingly enough, *Hyla vasta*, a tree frog nearly twice the size of *H. dominicensis*, also occurs throughout the areas from which came the Hispaniolan pellet samples; however, no bones attributable to *vasta* were present in any of the samples. This species, too, sits exposed at night and calls loudly. Also puzzling is the complete absence of frog remains in the skeletal samples

from Grand Cayman and the Bahamas, although *H. septentrionalis*, comparable to *H. dominicensis* in size and habits, occurs rather commonly on the Crooked-Acklins Bank in the Bahamas and on Grand Cayman (pers. obs.). Whether the absence of frogs other than *H. dominicensis* in the samples is an artifact of sampling or a reflection of some biologic factor is not known.

Invertebrates.—Johnston (1974) reported invertebrate remains along with vertebrate skeletal debris as indications of the food items of Barn Owls. Although I also found invertebrate remains in the form of crab and insect fragments in association with bone deposits, the reason for the presence of this arthropodan material is highly conjecturable, and I did not include such material in the analysis. I found no crustacean or insect fragments in any of the intact pellets.

SUMMARY

The Barn Owl appears to be a more opportunistic feeder in the southern Bahamas than on the North American continent. Although rodents are the predominant item of diet in both places, samples of food remains from the islands contain a higher proportion of non-rodent material, especially of birds, than do continental samples. These results probably reflect the lower abundance of rodents on islands.

Skulls representing new locality records for two species of birds (*Porzana carolina* and *Spindalis zena*) and two species of bats (*Lasiurus* sp. and *Artibeus jamaicensis*) are part of the skeletal debris collected at feeding sites of Barn Owls in the southern Bahamas.

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NEW LIFE MEMBER



Manuel A. Plenge is now a Life Member of the Wilson Ornithological Society. Mr. Plenge is a member of several scientific organizations and has published papers on the birds of western South America. He lives with his wife and son in Lima, Peru and is employed by a mining company. His hobbies include field hockey, photography, hunting, and trout-fishing.

SONGS IN CONTIGUOUS POPULATIONS OF BLACK-CAPPED AND CAROLINA CHICKADEES IN PENNSYLVANIA

RODMAN WARD AND DORCAS A. WARD

The whistled songs of the very similar and closely related Black-capped Chickadee (*Parus atricapillus*) and the Carolina Chickadee (*P. carolinensis*) are generally regarded as quite distinct. In southeastern Pennsylvania, the ranges of these two largely allopatric species are contiguous, with the Blackcap occurring in the northern sector and the Carolina in the southern. In an attempt to learn more about the distribution of song types, and presumably of the species themselves, we played taped songs to territorial chickadees in the area over five breeding seasons (extreme dates 17 April to 2 June) from 1963 to 1969. The songs of responding chickadees were tape-recorded, and notes were made on the behavior of the birds. We have classified these responses on the basis of the types of songs and on the composition of the song bouts recorded at each site. This paper presents these data, with an analysis and discussion of the findings and their possible significance.

STUDY AND METHODS

The study area is a rectangle bounded by latitudes 39° 53' N and 40° 13' N and longitudes 75° 45' W and 76° W; the area is approximately 22.5 miles from north to south and 13.25 miles wide (Fig. 1). It includes portions of Berks, Chester, and Lancaster Counties, Pennsylvania, and was selected to include breeding ranges of both species. The area is rural in setting and ecologically rather homogeneous. The wooded areas in the southern part more generally consist of farm woodlots and other small patches. The northernmost one-sixth of the study area is comprised to a large extent of rather rough, wooded state game lands and a state park. The natural vegetation is almost entirely deciduous growth, with a few small coniferous plantations, particularly in the north. Altitude ranges from 230 feet to 1,071 feet.

We broadcast pre-recorded, typical songs of one or the other of the two species from a Uher 4000S recorder at 87 localities (Fig. 1). We selected areas that appeared appropriate for nesting chickadees. The songs of any responding chickadee were recorded on a Nagra III recorder through an AKG dynamic microphone in a 24-inch parabolic reflector; tape speed was 15 in per sec. Comments on the type of songs broadcast and of the behavior of birds were also recorded, and written notes were frequently made. A limited number of audio-spectrograms were made on a Kay Electric Company Sona-Graph, using the narrow band filter to obtain as accurate a determination of frequencies as possible. Our Blackcap songs were from birds recorded in Berkshire County, Massachusetts, and the Carolinas were from New Castle County, Delaware.

In most cases the songs first broadcast were those of the species expected to be found in an area. This was an arbitrary decision, but we felt that response would occur more likely by playing the "local" rather than the other species' songs. Secondary broadcasts of the songs of the other species were frequently made when no reply was received or to test the response of a bird that had started its reply. Altogether, 97 recordings were

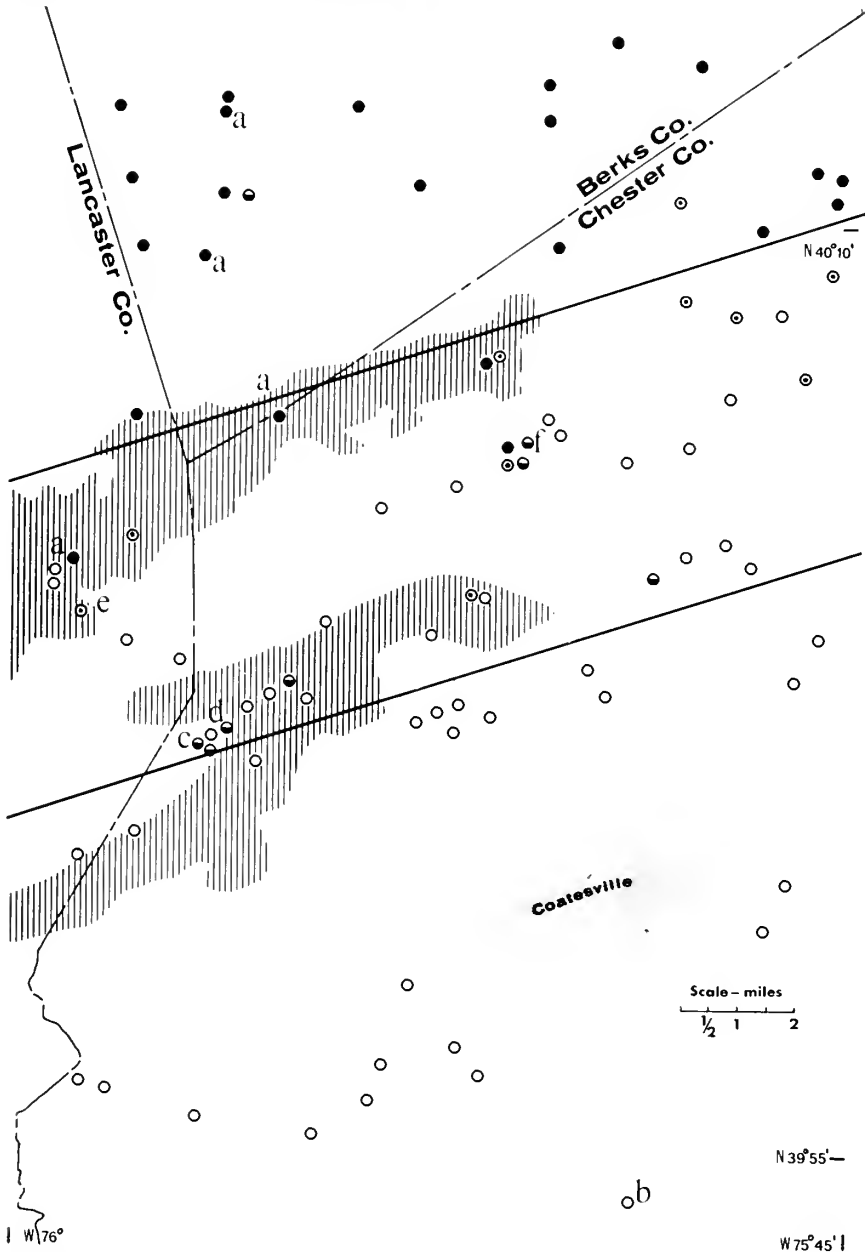


FIG. 1. Study area in three counties of southeastern Pennsylvania, showing northern, central, and southern segments (separated by heavier oblique lines), elevated areas (vertical slashing), and song types recorded (dot—Black-capped Chickadee songs only; half-black circle—Blackcap and Carolina songs; dotted circle—abnormal plus some Carolina songs; circle—Carolina songs only). Letters show text references.

made at the 87 locations. The ten repeated recordings were made in order to check further some unusual responses. Some of these rebroadcasts were one to two days after the original; in two or three cases the repeats were made two years later. All recordings made at one location are considered as one item in the analysis. Recordings were made from shortly after dawn until about noon.

CLASSIFICATION OF THE SONGS

A previous study of the songs of the Carolina Chickadee (Ward, 1966) showed wide variation in such parameters as number of notes per song, patterns of succession of notes in the higher and lower ranges of frequencies, and duration of notes. These variations were as great, or greater, among birds in Florida and in an area in tidewater Virginia, as among birds of regions closer to the Black-capped Chickadee's range. Every Carolina song recorded in that study included at least one note with a frequency (measured at its mid-point) higher than 4.7 kHz. The frequency at the mid-point seems to coincide closely with the pitch of the note, i.e. the frequency apparent to the ear. The high mid-point frequency in Carolina song is practically always distinguishable in the field from any frequencies heard in Blackcap song.

We have recorded songs of Black-capped Chickadees in Berkshire County and on Martha's Vineyard Island, Massachusetts, and in Monroe County and Centre County, Pennsylvania: we have listened to the songs in Alberta, British Columbia, California, Montana, New York, and Washington. In none of these places have we heard a chickadee song with a note pitched so high as to be confusable with the usual songs of the Carolinas. Our recordings do not show a note with a mid-point frequency above 4.3 kHz in Blackcap songs, and it is rarely above 4.0 kHz.

A three-noted song of the Black-capped Chickadee is frequently mentioned in the literature. We believe this refers to a fairly common form of the second note, in which occurs, in the middle of the note, a very short and sharp drop in the amplitude. Saunders (1946) says, "Frequently the second note has a slight waver in the middle, as if the bird sang *fee-beeyee* instead of *fee-bee*." The fact that there is no actual temporal break in sound is clear in the spectrograms that we have made of this form of note. These include songs of the species recorded by Dr. W. W. H. Gunn in Ontario, and which he kindly selected from his collection as showing this note form.

A considerable number of songs recorded by us contained frequencies in the range found in the Black-capped Chickadee, but included three, four, seven and eight notes. These we classify as distinctly abnormal, not safely attributable to birds of either species (Fig. 2).

Based on the above criteria, we have classified song types in our study into three categories: Blackcap, Carolina, and abnormal. Furthermore, we

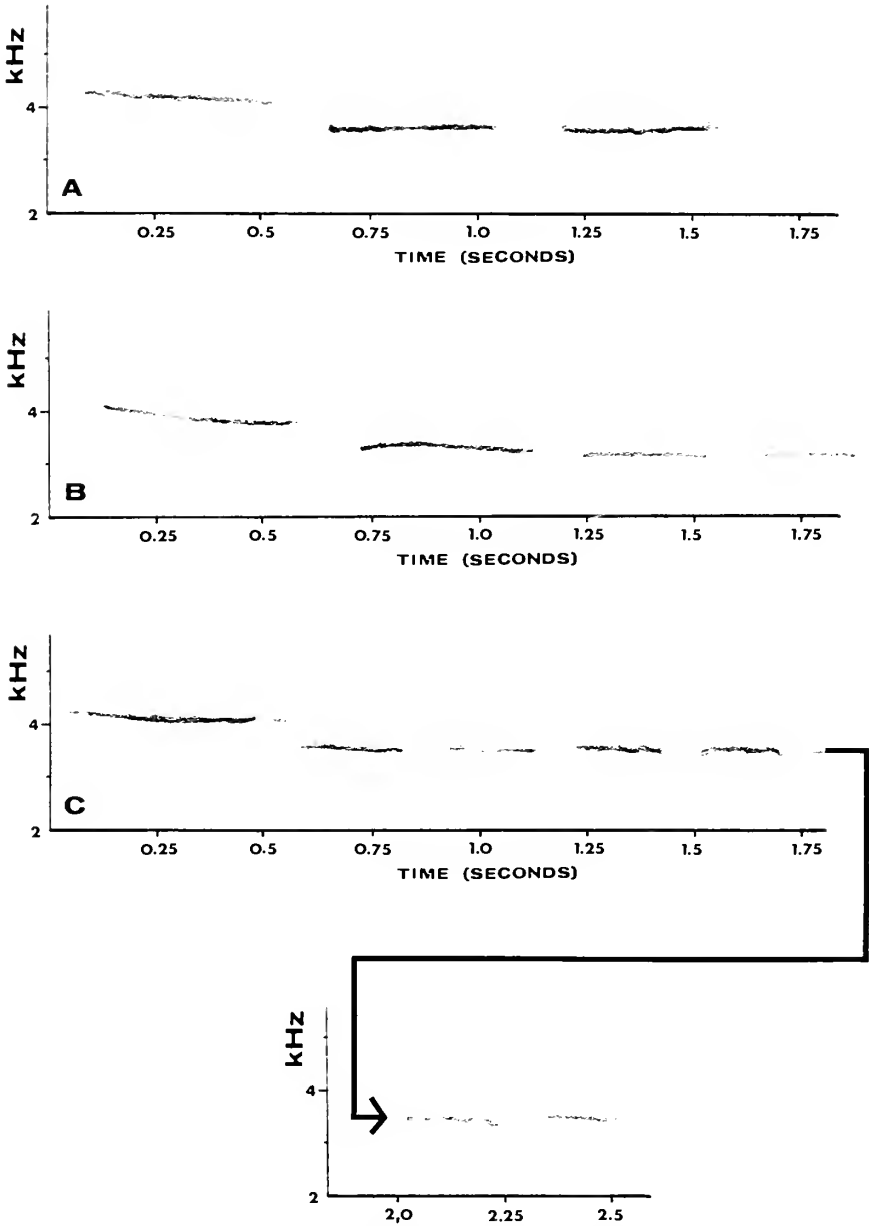


FIG. 2. Sonograms of abnormal chickadee songs from study area in southeastern Pennsylvania: A, three-noted song; B, four-noted song; and C, seven-noted song (shown in two parts). All of these songs are lower-pitched than those of Carolina Chickadees and have more notes than those of Blackcaps. Frequency (kHz) on vertical axis and time (sec) on horizontal axis.

have classified bouts of song into four categories: 1, consisting of only Blackcap songs; 2, consisting of Blackcap and Carolina songs (may include abnormal songs as well); 3, abnormal (may include Carolina songs as well); and 4, consisting of Carolina songs only.

RESULTS OF SONG PLAYBACK

We have plotted all of the 87 localities at which responses were recorded, to show the distribution of song types identified in the area (Fig. 1). Based on these responses, we find the study area divisible into three segments (Table 1): a northern one where Blackcap songs predominate; a central one in which the songs of both species are frequent and in which the abnormal songs are concentrated; and a southern one in which only Carolina songs were heard. The central segment includes all or major portions of Honeybrook, East and West Nantmeal, Wallace, and West Caln Townships in Chester County and Salisbury in Lancaster County. Prominent geological features of central segment are two east-west hogbacks, Welsh Mountain on the north and the Baron hills on the south (Fig. 1).

Before discussing the significance of the above findings, we would like to present some data on specific response to playbacks in the study area and elsewhere.

Response to playback by Carolina Chickadees south of the contact zone.— We tested for these responses in an area about twenty miles south of the study area, where we had never found indications of nesting Black-capped Chickadees in ten or more years experience. On 16 and 18 April 1970, we broadcast Blackcap songs, followed by two min of silence, then again broadcast and silence for two min. This procedure was repeated at six stations. On two alternate days, Carolina songs were substituted for the Blackcap broadcasts, in the same format of testing.

Only one recognizable reaction by chickadees to broadcasts of Blackcap

TABLE 1
DISTRIBUTION OF SONG TYPES IN THE STUDY AREA

| Song types recorded | Segments of the study area | | |
|--|----------------------------|---------|----------|
| | Northern | Central | Southern |
| Black-capped Chickadee (only) | 19 | 4 | 0 |
| Black-capped and Carolina Chickadee ¹ | 1 | 7 | 0 |
| Abnormal ² | 1 | 9 | 0 |
| Carolina Chickadee (only) | 0 | 22 | 24 |

¹ May include some abnormal song.

² May include some Carolina, but no normal Blackcap song.

song occurred. Two chickadees appeared after the second broadcast, one of which sang "faint, tentative, high-pitched, two-noted songs." A third broadcast brought these birds back and incited a faint reply. A fourth broadcast brought the birds back again but with no reply song. The broadcasts of Carolina song produced aggressive replies at four stations. These included continuing song, agonistic calls, and flight back and forth close to the recorder apparently in search for the intruder.

These findings suggest that in these Carolina Chickadees the reaction to song is primarily species-specific away from the zone of contact, even when the distance is only a score or so miles. From this response, we theorize that song is a species attribute of the Carolina and probably of the Blackcapped Chickadee, at least away from the areas of near or actual contiguity.

Inter-specific response to song playback.—At four locations (Fig. 1, a) in the study area, playbacks of Carolina songs brought in birds that responded only with Blackcap songs. These localities are in, or within, $4\frac{1}{2}$ mi of the central sector of the study area, where the songs of both species—as well as abnormal songs—were heard. At another locality (Fig. 1, b), broadcast of Blackcap songs brought in a bird that replied with the common four-noted Carolina song. This site is in the southern segment of the study area, approximately ten mi south of the nearest locality where Blackcap song was heard.

In and near Pigeon Swamp, Middlesex County, north-central New Jersey, we discovered one bird singing Carolina songs and three birds singing Blackcap songs (one of the latter including abnormal songs). One bird, singing only normal Blackcap songs, approached very closely on our playing of Carolina songs, and it continued singing Blackcap songs. From the bird's continued singing and excited flying back and forth, we assumed that it was responding to Carolina songs, in an attempt to drive the intruder from his territory.

From these observations, we conclude that as the ranges of these two species approach each other, some cognizance of the song of the opposite species appears to come into play. In other words, the two species may become responsive to both songs, rather than just their own.

Responding birds singing the songs of both species.—At eight localities (Fig. 1) in our Pennsylvania study area, we recorded single birds singing audio-spectrographically normal songs of both Black-capped (Fig. 3) and Carolina (Fig. 4) Chickadees. A few of these birds also included some abnormal songs in their performance, i.e. of the low Blackcap pitch but with three to eight notes. At ten localities (Fig. 1), single birds sang abnormal songs, in some cases mixed with Carolina but never with Blackcap songs (Fig. 2).

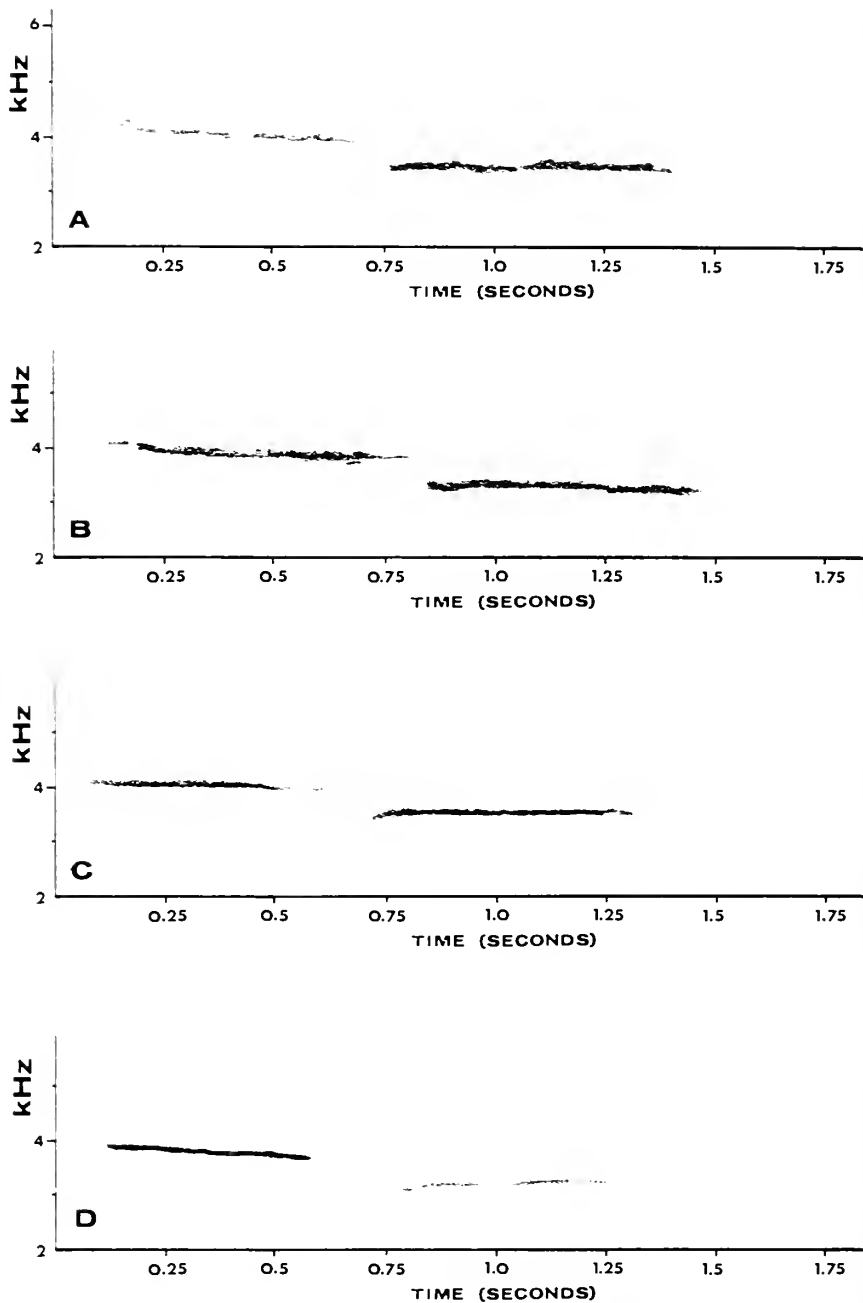


FIG. 3. Sonograms of Black-capped Chickadee songs: A, from Massachusetts; B, from Pocono Mountains, Pennsylvania; and C-D, from study area in southeastern Pennsylvania (these same individuals also sang typical Carolina songs, as shown in Fig. 4, C-D).

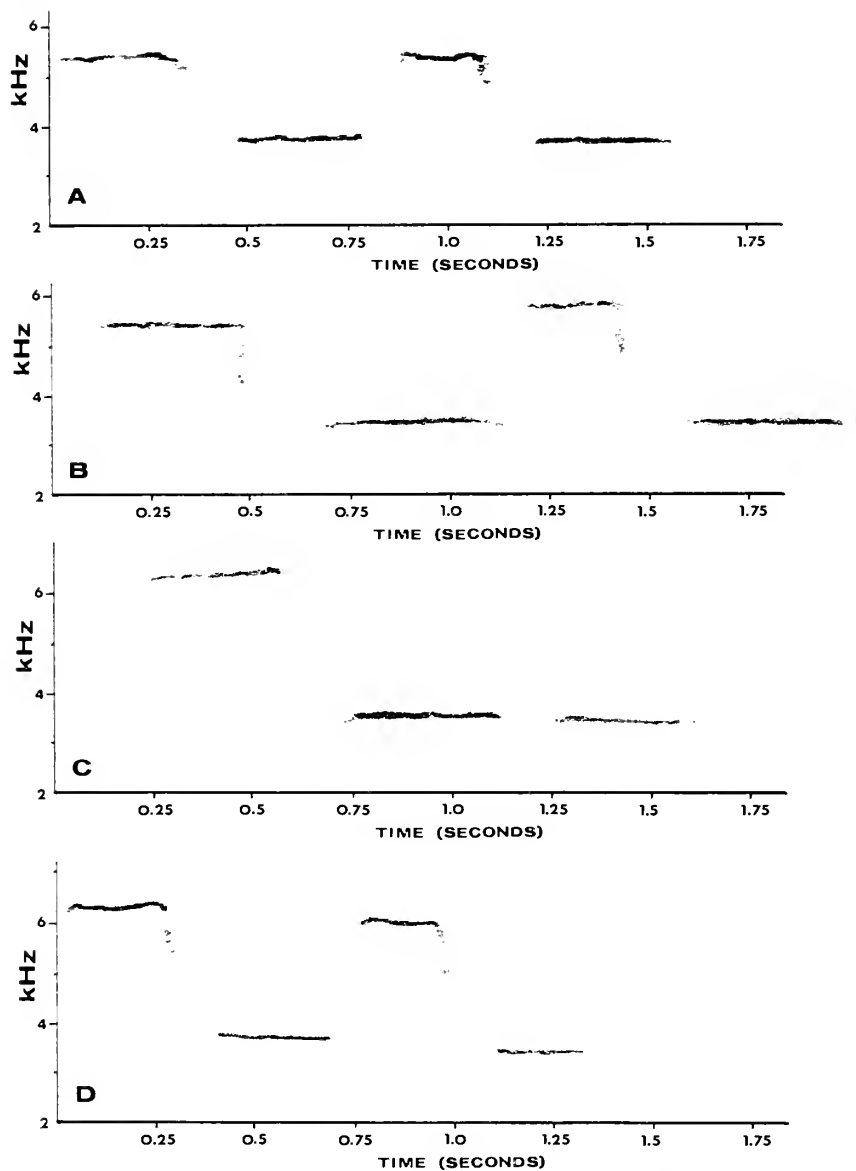


FIG. 4. Sonograms of Carolina Chickadee songs: A, from Delaware; B, from South Carolina; and C-D, from study area in southeastern Pennsylvania (these same individuals also sang typical Blackcap songs, as shown in Fig. 3, C-D).

In the birds that sang songs of both species, or of Carolina and abnormal types, we could find no evidence that the type of song broadcast has any influence on the replying types of songs. In nine such birds, five replied first in the idiom of the broadcast and four in the opposite.

At one location (Fig. 1, c) broadcast of Carolina songs attracted a bird that sang seven entirely typical Carolina songs, but without further broadcast it changed to a series of eleven normal Black-capped songs and four single-noted songs in the low pitch range. At the same location two days later, broadcast of Carolina songs again started Carolina reply, and again the bird changed to Blackcap songs without our further broadcasting.

At another locality (Fig. 1, d), a bird replied with normal Blackcap songs to a broadcast of Blackcap songs. We interrupted this with a broadcast of Carolina songs to which the bird replied with Carolina songs. It continued Carolina songs in spite of additional Blackcap broadcast.

A third example of this kind of reaction was provided at a locality (Fig. 1, e) at which a bird was incited to sing an abnormal song in response to broadcast of Blackcap songs. With no change in our broadcast the bird shifted to somewhat unusual Carolina songs. Eventually it moved away, but additional broadcast of Blackcap songs brought it back, singing the original abnormal song.

On the other hand, on two successive days at one location (Fig. 1, f) broadcast of Carolina songs attracted a bird that first replied with normal Blackcap songs and, without prompting, then changed to Carolina songs. The contemporaneously recorded comment on another occasion was, "This bird was started singing by our broadcasting Carolina song, and he started with the Black-capped song. Subsequently he sang Carolina, to some extent while we were broadcasting Black-capped song."

In May 1965, at Big Meadows, Shenandoah National Park, Virginia, our broadcast of Carolina songs brought in a pair of birds, one of which sang a series of Blackcap songs. The bird then changed to somewhat unusual Carolina songs, the shift occurring "quite a while after we had played back anything to him." After an extended period without any song from the bird, broadcast of Carolina songs again drew the pair back again, and one of them sang additional Blackcap songs. From time to time during this episode we heard another bird singing Carolina songs at a distance.

At Pigeon Swamp, New Jersey, a broadcast of Carolina songs started Blackcap reply. Eleven normal songs interspersed with seven three-noted songs in the Blackcap pitch range were recorded. We were preparing to leave when the bird changed to typical Carolina songs. We then recorded 15 more songs, all Carolina except for one normal Blackcap song.

DISCUSSION

The breeding ranges of the Black-capped and Carolina Chickadees are essentially contiguous from New Jersey to Kansas and in parts of the Appalachian Mountains. In some areas of the Midwest and southern Appalachians, respectively, there are gaps between the ranges of two species of a few miles (Brewer, 1963) or a few hundred feet in altitude (Tanner, 1952). In Kansas (Rising, 1968), other parts of the Midwest (Brewer, *op. cit.*), and in western Virginia (Johnston, 1971), the two forms meet and apparently hybridize—at least to some extent.

As already mentioned, the songs of the two species are generally distinct. In addition, the *dee-dee-dee* and *tsicka-dee-dee-dee* calls are usually distinguishable, those of the Blackcap being lower in pitch and given more slowly. However, the songs are the most distinctive, and these we have concentrated on in our study. In the Black-capped Chickadee, Dixon and Stefanski (1970) point out that songs are employed mainly by the male in maintenance of a claimed or occupied nesting territory—not, at least on a regular basis, to advertise for a mate. Brewer's (1961) assessment of the function of song in this species is similar to the above, as is that of Smith (1972) for the Carolina Chickadee.

The question of what happens to the songs of the two species in areas of contact has not been probed in detail, although authors such as Brewer (1963), Rising (1968), and Johnston (1971) draw attention to vocal anomalies in such areas. Our study has shown that anomalies also occur in the zone of presumed contact between these two species in our study area in southeastern Pennsylvania (and elsewhere). Basically, the anomalies are of two types: 1, intergradation, i.e. instances in which a bird sings songs that are both low-pitched (Blackcap trait) and composed of more than two syllables (Carolina trait); and 2, duality, i.e. instances in which a bird perfectly sings the songs of both Black-capped and Carolina Chickadees. A variant is where these two types are combined, i.e. a bird sings intergrade as well as the songs of both species or of the Carolina Chickadee.

In areas such as the Midwest (Brewer, 1963), Kansas (Rising, 1968), and Virginia (Johnston, 1971), anomalies in songs of these two species appear to result from hybridization. Such could also be the case in southeastern Pennsylvania, although we have no specimen data to assess this possibility. There is also a problem in equating vocal anomalies reported from hybrid zones by various workers—none of whom tape-recorded their birds—with the anomalies that we found. For example, Brewer's (1963) findings appear to differ from ours in two ways: 1, he reported that about half the birds in his zone of contact and hybridization sang *only* aberrant (= intergrade) songs; and 2, he reported no instance of a bird singing the songs of both

species. We found, on the other hand, that only about 21 percent of the birds in the presumed area of contact sang intergrade songs (Table 1), and of these several birds also sang Carolina songs. In addition, about 17 percent of the birds in this area of southeastern Pennsylvania sang the songs of both species. Precisely what the differences signify between our data and those of Brewer, we are unable to say. However, the differences do suggest that some caution is needed before blanketly ascribing the anomalies in songs to hybridization, at least in regards to our areas of investigation.

Although hybridization is perhaps the most likely cause for vocal anomalies in chickadee songs that we found (e.g. in southeastern Pennsylvania), it is not the only possible explanation. We would like to raise one other possibility, that being that the two species could be responding to contact by developing some degree of vocal convergence and mimicry. We admit that the evidence for this theory is scant, but we feel that it deserves some attention.

Earlier we cited several workers who reported that the main function of song in these two species is to defend a territory—rather than to attract a mate. In addition, Brewer (1963) has suggested that where the two species come in contact, they are interspecifically territorial. In fact, he found evidence in the Midwest that chickadees defended their territories against both species and any hybrids.

Given that the two species might be interspecifically territorial, one can envision that song might play an important role in this activity—at least in some areas. Furthermore, it would be conceivable that to facilitate vocal defense of territories, chickadees in an area of contact would mimic each other's songs and even converge to some degree, i.e. develop intergrade songs. Enhancing the supposition that mimicry and convergence might be occurring is the fact that such behavior would not interfere with mate selection, because the song is a repelling rather than an attracting agent.

Interestingly, in the hybrid zone in Virginia, Johnston (1971) took a bird that sang the songs of both species, and the specimen proved to be (at least mensurally) nearest the Carolina Chickadee. In the Great Smoky Mountains, Tanner (1952) also found a chickadee singing both songs; although he was unable to collect the bird, among other specimens from there he found no evidence of hybridization between the two species.

As a point of interest, a duality in song has also been found among interspecifically territorial species (and non-hybrid individuals) of meadowlarks (*Sturnella* spp.) by Lanyon (1957:23–26) and towhees (*Pipilo* spp.) by Marshall (1964) and Cody and Brown (1970). The latter authors and Cody (1970) provide discussions on vocal convergence (including mimicry), and we shall not elaborate on the subject further. Suffice to say, in raising mimicry convergence as an alternative to hybridization to possibly explain anom-

alies in songs in our study area, we are mainly concerned with pointing out the need for a broader inquiry into the subject. As a matter of opinion, we feel that hybridization is indeed the most likely explanation for our results, but the issue is far from closed.

SUMMARY

Playback broadcasts were made of Black-capped and Carolina Chickadee songs during five breeding seasons in southeastern Pennsylvania. Responding chickadees were recorded at 87 different localities and their songs and song bouts were classified. We found a predominance of Blackcap song in the north of our study area and of Carolina song in the south; birds in the central segment sang songs of both species and sometimes songs that were abnormal in some way. We discuss two explanations for the situation in the central segment: one, the songs may reflect interbreeding; two, the two species may be interspecifically territorial in the area of contact, with individuals giving both species' and abnormal songs in defense of their territories.

ACKNOWLEDGMENTS

We wish to thank Charles G. Sibley for suggesting this investigation in our area and John Hubbard for valuable suggestions and for comments on the various drafts of this paper. The Laboratory of Ornithology of Cornell University provided the Nagra recorder and Crawford H. Greenewalt made available his Sona-Graph for our use.

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COMPETITIVE RELATIONSHIPS AMONG KINGBIRDS (*TYRANNUS*) IN TRANS-PECOS TEXAS

HARRY M. OHLENDORF

The Western Kingbird (*Tyrannus verticalis*) and Cassin's Kingbird (*T. vociferans*) are conspicuous elements of the summer avifauna in the Trans-Pecos region of Texas. These species were selected for a study of possible competitive relationships among sympatric species because of their similarities and abundance.

The approach in this study was to examine the ways in which the resources of the area were divided among the two kingbird species. Three principal aspects were examined: utilization of different resources, using the same resources at different places, and obtaining the same resources in different ways. The Trans-Pecos is the most physiographically varied portion of Texas (Blair, 1950), and the resultant ecological diversity makes the area especially suitable for studies of this type (see Orians and Willson, 1964).

METHODS

Field work was conducted from June through August 1969 and May through August 1970, with supplemental observations in November 1970 and May 1971. Survey trips were made throughout the Trans-Pecos area to determine the geographical and ecological distribution, nesting habits, and food consumption of the kingbirds, as well as to study the habitat types of the area. More detailed studies were carried out at selected sites. Literature and museum locality records supplement the distributional data of this study. One other nesting record was obtained from the North American Nest-record Card Program.

Kingbirds were caught and then banded with colored plastic (and with aluminum Fish and Wildlife Service) leg bands. Color-banded birds were watched to learn about their daily activities, including behavior toward other flycatchers. Birds were captured with mist nets by using a stuffed Great Horned Owl (*Bubo virginianus*) as a decoy.

Specimens for food analysis were shot, weighed, and the hour of collection was usually recorded. They were then injected with 10 percent formalin to stop digestion. Digestive tracts were then used for laboratory analysis of the diet. Food items were identified, counted, and then measured by volumetric displacement. Items displacing less than 1 ml of water were measured in a 2 ml syringe graduated to 0.1 ml; volume was determinable to the nearest 0.025 ml. Larger items were measured in a 15 ml centrifuge tube. The material contained in the stomach (proventriculus and ventriculus) of an individual bird is defined here as a sample. In addition to absolute values, percent values were calculated for each measurement. The latter are considered more informative in determining similarities and differences in composition and allow comparison of unequal numbers of samples.

Botanical nomenclature follows Correll and Johnston (1970). Habitat data were analyzed by appropriate methods presented in Snedecor and Cochran (1967). Means and 95 percent confidence intervals were calculated for measurement data, and chi-square and t-test analyses were generally used to determine statistical significance.

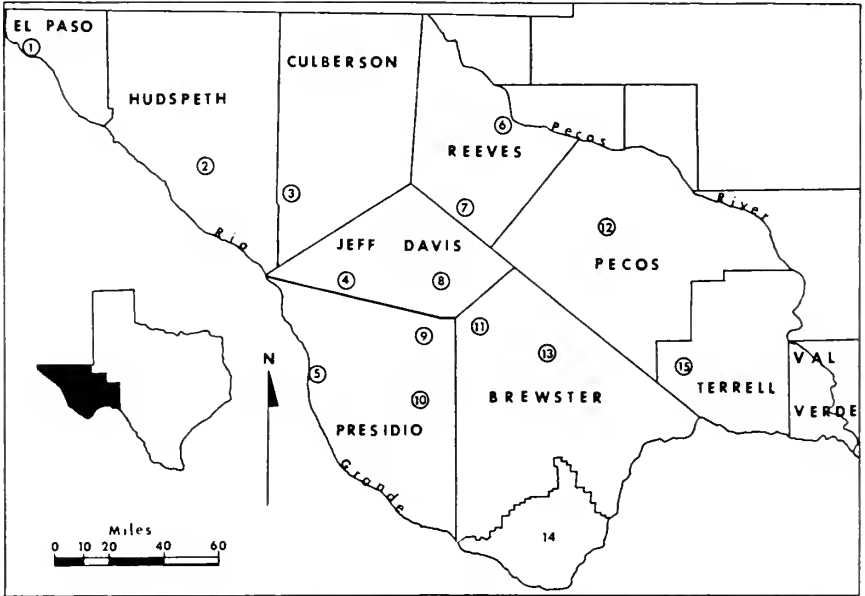


FIG. 1. Map of the Trans-Pecos region. Principal localities are indicated as follows: El Paso (1), Sierra Blanca (2), Van Horn (3), Valentine (4), Candelaria (5), Pecos (6), Balmorhea (7), Fort Davis (8), Marfa (9), Plata (10), Alpine (11), Fort Stockton (12), Marathon (13), Big Bend National Park (14) and Sanderson (15).

DESCRIPTION OF STUDY AREA

The Trans-Pecos, an area of some 32,000 square miles, encompasses a variety of habitat types, including the most arid and the highest areas of Texas. It is situated west of the Pecos River, north of the Rio Grande, and south of New Mexico (Fig. 1). Basic geologic features are an alternation of mountain ranges and alluvium-filled bolsons, with the eastern quarter of the area (Terrell, southern Pecos, and northeastern Brewster Counties) comprised of rolling to broken country known as the Stockton Plateau. Elevations range from 1,200 ft. in Terrell County, to 8,751 ft. in northwestern Culberson County.

Principal mountain areas are the Guadalupe, Davis, and Chisos ranges. The Guadalupe form an extension (about 20 mi long) into Texas of the mountainous regions of New Mexico. Their biological significance is due primarily to their great elevation rather than to the size of the area which they occupy. The Davis Mountains occupy an extensive area of Jeff Davis County, with elevations of 6,000-8,382 ft. Elevations reach 7,835 ft in the Chisos Mountains, located within Big Bend National Park (Brewster County).

Most of the region is drained by the Rio Grande, the Pecos River, and their tributaries. An extensive area in north-central Presidio, western Jeff Davis, western Culberson, and much of Hudspeth Counties has no exterior drainage, the runoff forming shallow salt lakes.

Rainfall for the Trans-Pecos region averages 12 in per year. Amounts are generally less at lower and greater at higher elevations, with a maximum of 18 in in the Davis Mountains (Orton, 1969). July, August, and September are generally the months of

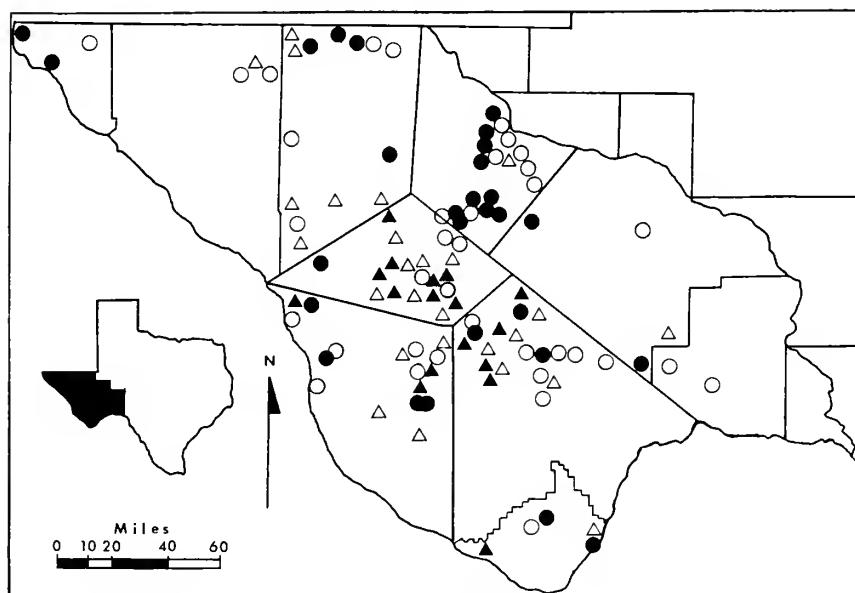


FIG. 2. Breeding distribution of *Tyrannus verticalis* and *T. vociferans* in the Trans-Pecos region. Dots and circles are summer localities for *verticalis*; solid triangles are nesting and open triangles are summer localities for *vociferans*.

greatest precipitation, although great annual and seasonal variations occur; precipitation-free periods of several months are normal (Orton, 1969). Average annual temperatures range from 58°F in the Davis Mountains to 70°F at Presidio.

The biota of the region is typical of the Chihuahuan Desert (Blair, 1950), and most of the area remains natural, modified by grazing of livestock. Considerable vertical zonation exists in vegetative types. Desert shrub is the predominating type up to 4,000 or 5,000 ft; grassland and pine-oak-juniper types occur above this elevation. Cultivated areas are generally confined to irrigated valleys, e.g. at El Paso, Presidio, Balmorhea, and near Pecos.

Desert shrub is composed primarily of creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), ocotillo (*Fouquieria splendens*), and acacias (*Acacia* spp.). Washes support more robust forms of these shrubs and mesophytes, such as desert willow (*Chilopsis linearis*) and baccharis (*Baccharis* spp.). Grasses are short and sparse.

Mountain grasslands occupy plains and intermontane valleys at 4,000–6,000 ft in Jeff Davis, northern Presidio, and Brewster Counties. The grasses *Bouteloua* spp., *Sporobolus* spp., *Bothriochloa* spp., and *Leptochloa dubia* are among the more important, with *Bouteloua ramosa* and *Hilaria nutica* more common in arid areas. Yuccas (*Yucca* spp.) and cholla cacti (*Opuntia* spp.) are especially common where the grasslands grade into desert shrub, although they also occur elsewhere throughout the region.

The principal woody species are at altitudes above 5,000 ft and constitute the pine-oak-juniper type. Oaks (*Quercus grisea*, *Q. emoryi*) and junipers (*Juniperus* spp.) are most common at the lower elevations. Pinyon pine (*Pinus edulis*) is abundant above 6,000 ft and replaces the oaks.

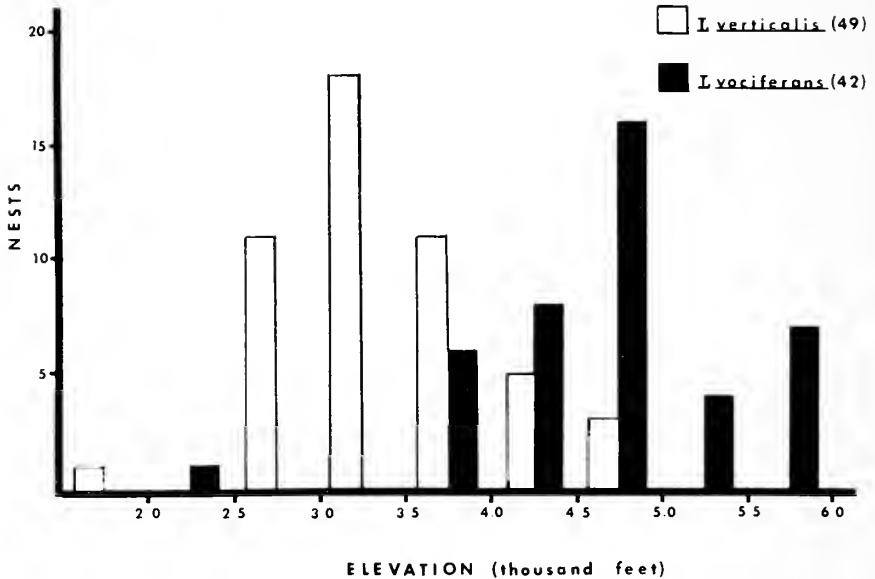


FIG. 3. Distribution of *Tyrannus* nests relative to elevation.

Riparian vegetation forms a gallery generally less than 100 ft wide in streambeds. Typical trees are cottonwoods (*Populus* spp.), willows (*Salix* spp.), ash (*Fraxinus* spp.), and walnuts (*Juglans* spp.); baccharis and willows are common shrubs.

DISTRIBUTION AND HABITAT

Both species of kingbirds are at the margins of their distributions in the Trans-Pecos region. This area represents, for this portion of their ranges, the southern breeding limit for *T. verticalis* and the eastern limit for *T. vociferans*. These are the only regularly breeding members of the genus in the area (A.O.U., 1957; and other sources). The Eastern Kingbird (*T. tyrannus*) occurs as a migrant, whereas two southern species (*T. melancholicus* and *T. crassirostris*) are rare visitors in the Big Bend area (Wauer, 1973). The breeding distribution of *T. verticalis* and *T. vociferans* in the study area is shown in Fig. 2. There they are locally common, although less abundant than reported in southeastern Arizona by Hesperheide (1964).

The kingbirds arrive in the area as early as mid-April, with nest construction commencing in early May. In general, birds remain in nesting areas from about 10 May to 10 August. Therefore, only localities at which birds were recorded in this period are considered as breeding localities. Nesting localities referred to in this paper are those at which attended nests or fledglings incapable of extended flight were found.

TABLE 1
DISTRIBUTION OF *TYRANNUS* NESTS RELATIVE TO HABITAT TYPE

| Habitat | Number of nests per habitat type | | | |
|--------------------------------|----------------------------------|---------------|----------------------------|---------------|
| | <i>verticalis</i> (n = 47) | | <i>vociferans</i> (n = 42) | |
| | Natural site | Manmade site* | Natural site | Manmade site* |
| Pine-oak-juniper | — | — | 2 | 1 |
| Total (percent of total nests) | — | | 3 (7.1%) | |
| Grassland | — | 3 | — | 5 |
| Grassland-shrub | 1 | 2 | 3 | 4 |
| Grassland-juniper | — | 1 | — | 2 |
| Grassland-oak | — | — | 6 | 2 |
| Total (percent of total nests) | 7 (14.9%) | | 22 (52.4%) | |
| Desert shrub | 1 | 17 | — | 5 |
| Total (percent of total nests) | 18 (38.3%) | | 5 (11.9%) | |
| Farmland | — | 19 | — | — |
| Total (percent of total nests) | 19 (40.4%) | | — | |
| Riparian, flanked by | | | | |
| Grassland | — | — | 2 | — |
| Grassland-shrub | — | — | 2 | — |
| Grassland-oak | — | — | 4 | — |
| Desert shrub | 1 | — | 2 | — |
| Total (percent of total nests) | 1 (2.1%) | | 10 (23.8%) | |
| Suburban | — | 2 | — | 2 |
| Total (percent of total nests) | 2 (4.3%) | | 2 (4.8%) | |

* Nesting presumably in response to the presence of utility lines or trees associated with houses, fences, and roadside parks.

Altitudinal segregation among nesting localities of the two species is easily seen (Fig. 3), based on 49 nests of *verticalis* and 42 of *vociferans*. Forty-one (83.7 percent) of the *verticalis* nests were at elevations of less than 4,000 ft, whereas 35 (83.3 percent) of those of *vociferans* were at elevations exceeding 4,000 ft. The mean elevation of *verticalis* nests was $3,332 \pm 133$ ft; mean of *vociferans* was $4,735 \pm 229$ ft. Comparison of these means indicates that the difference is highly significant (t-test, $P < 0.01$).

Differences in altitude of nesting are associated with differences in habitat usage, based on 47 nests of *verticalis* and 42 of *vociferans* (Table 1). Thus, all kingbird nests (3) in the pine-oak-juniper habitat type were of *vociferans*, although these represented only 7.1 percent of the nests for this species. In habitats where overlap occurred, one species or the other was dominant. In

grassland and riparian situations, *vociferans* was the dominant species, but *verticalis* dominated in the desert shrub and farmland areas. The construction of telephone and power lines and the planting of trees associated with houses, fence rows, and roadside parks generally favored the nesting of kingbirds. Those nests designated in various habitats as "manmade" (Table 1) were thought to be situated there only because of such human-related modifications. Distributional differences in shared habitat types (i.e. grassland, desert shrub, riparian, and suburban) are highly significant (χ^2 , $P < 0.01$).

Nesting records and breeding season locality records for the two species in Jeff Davis County and the surrounding area serve to illustrate species segregation (Fig. 2). *Vociferans* predominated overwhelmingly in the pine-oak-juniper, grassland, and riparian habitats of Jeff Davis County, where elevations generally exceed 5,000 ft. *Verticalis* occurred essentially alone at elevations less than 3,500 ft in the desert shrub and farmland of adjacent Reeves County. Other portions of this area had intermediate elevations and were occupied by both species.

Post-nesting dispersal is apparent after early August. Subsequent to then, birds are more frequently observed in areas which do not afford nesting substrate, but which are used for feeding. Counts were made periodically on a route of 74.5 mi along Texas highways 17, 118, and 166 west of Fort Davis. The route transects grassland and pine-oak-juniper types, ecotones of these, and also grassland-desert shrub. Both species, but especially *vociferans*, were more abundant in August. Four trips during May through July 1969 and 1970 yielded one *verticalis* and 128 *vociferans* individuals, whereas an equal number of trips during August 1969 and 1970 yielded six *verticalis* and 511 *vociferans*. The birds utilized fences and telephone lines as feeding perches and were usually not in close proximity to any suitable nesting substrate in August.

NESTING

Kingbirds nested in a variety of sites, but nests were usually located in trees when these were available. The more frequent use (χ^2 , $P < 0.05$) by *verticalis* of man-made structures is a reflection of the species' occurrence in situations where trees were fewer. Eighteen (38.3 percent) *verticalis* nests and five (11.9 percent) *vociferans* nests were located on man-made structures. Twenty-one of these nests were situated on utility poles. Thus, only 57.4 percent (27) of *verticalis* nests were in trees, compared to 78.6 percent (33) of *vociferans* nests. The most frequently used trees were cottonwoods for both of the kingbird species.

Nests of *verticalis* were generally closer to the ground. While 82.6 percent (19) of the *verticalis* nests were at heights of less than 30 ft (mean of tree

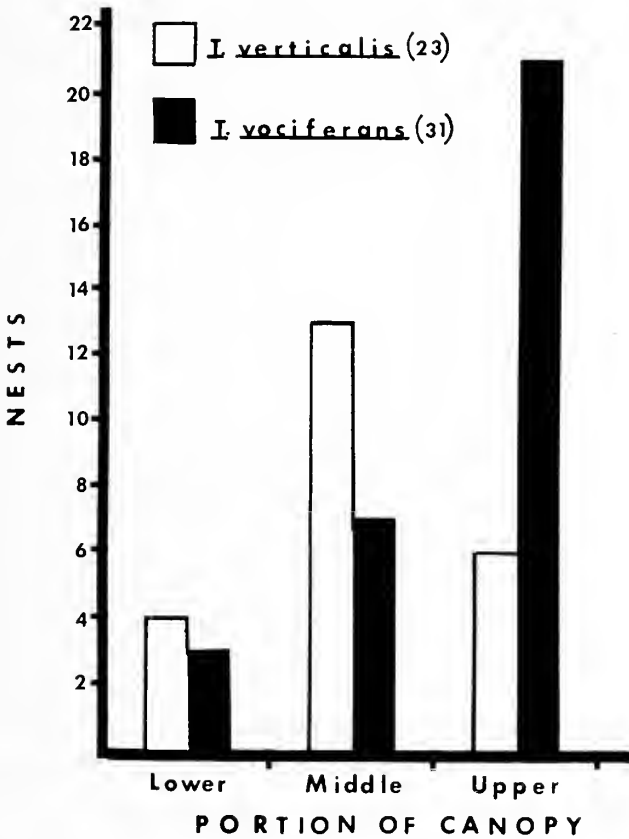


FIG. 4. Relative portion of tree canopy in which *Tyrannus* nests were located.

nests 21.0 ± 3.4 ft), only 48.4 percent (15) of the *vociferans* nests were that low (mean 29.3 ± 4.2 ft). The difference between these means is highly significant (t-test, $P < 0.01$).

Differences also existed among tree-nesting kingbirds as to the portion of the canopy (i.e. lower, middle or upper third) in which the nests were situated (Fig. 4). Whereas *verticalis* tended to nest in the middle third (56.5 percent), *vociferans* nested significantly (χ^2 , $P < 0.01$) more frequently (67.7 percent) in the upper third. Hence, when nesting in trees, *verticalis* tended to nest lower than *vociferans*, regardless of tree height.

Verticalis tolerated closer spacing of nests than did *vociferans*, with nests of the former as close as 90 ft in roadside cottonwood trees west of Fort Stockton, 180 ft at Plata, and 195 ft near Balmorhea. Although these were highly modified situations, with large trees planted and maintained in desert

shrub or farmland habitat types, they do demonstrate the degree of tolerance in nesting. In grassland-shrub and desert shrub not so highly modified by man (northern Culberson County), *verticalis* nests were located as close as 0.2 mi to each other.

In *vociferans*, nests were not observed nearer than 675 ft; in another instance separation was 1,650 ft. Both of these cases occurred in riparian vegetation flanked by grassland-shrub, south-southeast of Alpine. Interspecifically, i.e. *verticalis* and *vociferans*, nests were located within 35 ft of each other at Plata. Although the *vociferans* nest failed, the failure was apparently due to wind and not to the presence of *verticalis*. In another instance, east-northeast of Alpine, interspecific separation was 135 ft. In general, nests were seldom located this close, because the two species so infrequently occurred together during the breeding season.

Nest construction by *verticalis* was observed as early as 6 May and as late as 9 July, compared to 11 May and 6 July for *vociferans*. Two individuals of *verticalis* were brooding as late as 21 July; as young remain in the nest for about two weeks, nestlings of this species probably occurred as late as 5 August. An adult *verticalis* was seen feeding fledglings on 13 August, and in *vociferans* nestlings were recorded on 12 August. These data indicate a similar breeding chronology for the two species.

Means and ranges of clutches were 3.3 (1 to 5) in 14 *verticalis* and 3.3 (2 to 4) in 15 *vociferans* nests. Successful rearing of more than one brood by the same adults was not observed. However, in one instance when the first nest was lost, a second was constructed and young were raised.

FEEDING

Both kingbird species apparently fed on prey that was most readily available, although I do not have data pertaining to the abundance of prey taxa. Because of this lack, any interpretation of competition for food having existed between *verticalis* and *vociferans* is not subject to proof. However, an analysis of samples taken during the study serves to illustrate similarities and differences in the diets of the birds.

Percent occurrence (presence or absence), percent individuals (numbers of individuals), and percent volume (size of food items) are considered useful in analyzing the samples. Values less than 0.1 percent were considered "traces" and represent volumes less than 0.025 ml. Percent occurrence generally indicates the consistency in selection of a taxon. Taxa with the greater occurrence were those taken frequently, but this gives no indication of the relative number of individuals taken. Therefore, it is necessary to consider percentage of individuals. However, small types may be taken relatively often and in fairly large numbers without constituting a major portion of the diet.

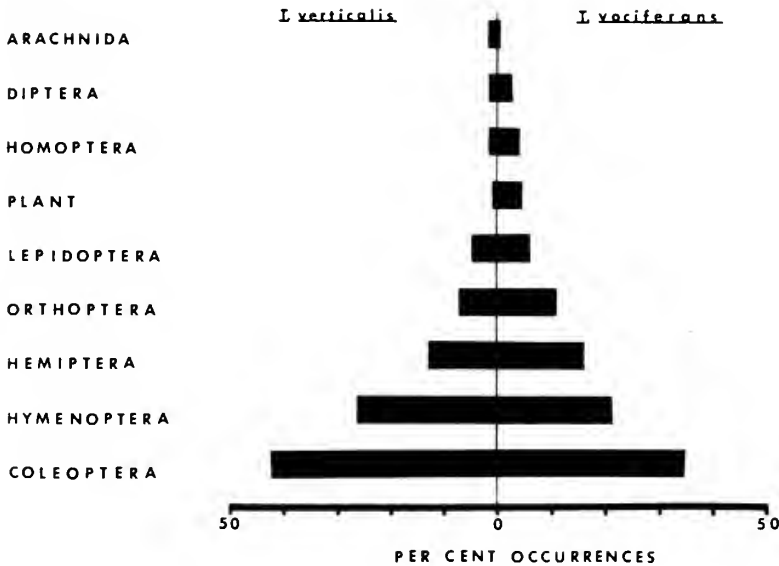


FIG. 5. Relative frequency, expressed as percent total taxon occurrences, of major prey types in *Tyrannus verticalis* (n = 48) and *T. vociferans* (n = 79) samples. Symmetry indicates similar diets of these birds.

Percent volume serves to indicate the true importance of each taxon, although this is easily influenced by the recency of consumption and rapidity of digestion for the particular food item.

All insect tissues are similar in terms of calories per ash-free gram (Slobodkin, 1961). Consequently, differential nutritive values per unit are not a factor. Although no effort was made to assess the energy expended in foraging for the various prey, it seems reasonable that the taxa representing the greatest portion of the volume constitute the most important taxa of the diet.

Analysis of food composition is based on 48 samples of *verticalis* and 79 of *vociferans*. Most food items could be identified to family. Both kingbirds were found to be principally insectivorous (97.5 percent in *verticalis*, 94.6 percent in *vociferans*), but arachnids and plant material were also consumed. The plant material in both species was comprised of fleshy fruits (Rhamnaceae) and seeds (Anacardiaceae). *Verticalis* had a mean of 4.1 ± 0.6 taxa (including plants) per sample, whereas *vociferans* had 3.8 ± 0.5 taxa. The diet of *verticalis* may be somewhat more diverse, but the difference is not significant (t-test, $P > 0.2$).

The relative occurrence of major prey types is very similar in these two species, as is reflected by the symmetry in the profiles of their diets (Fig. 5).

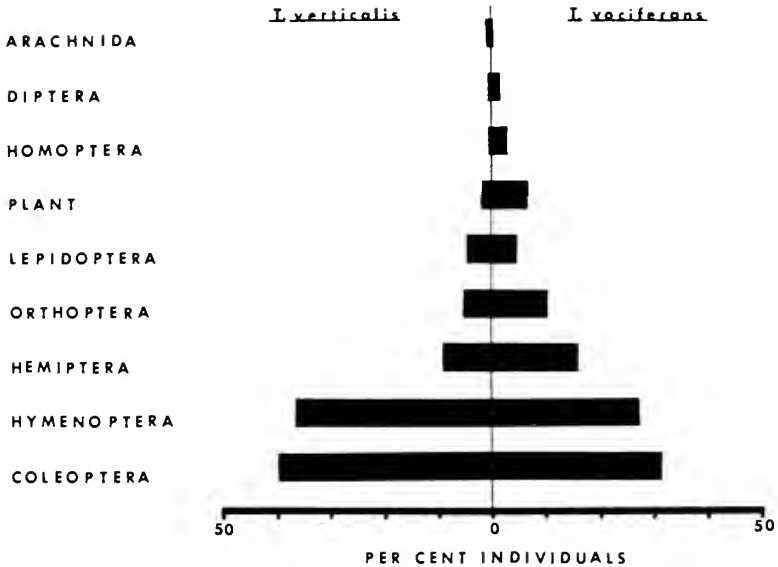


FIG. 6. Relative number of individuals, expressed as percent total individuals, of major prey types in *Tyrannus verticalis* ($n = 48$) and *T. vociferans* ($n = 79$) samples. Symmetry indicates similar diets of these birds.

The extent of overlap in diets may be expressed quantitatively by the formula of Bray and Curtis (1957), modified as: percent overlap = $(2 \text{ times shared taxa}) \times 100 / \text{sum of taxa in } verticalis + \text{sum of taxa in } vociferans$.

Contrasted to the finding of complete overlap in diet based on major prey types (i.e. insect orders, arachnids, and plant material), the above calculation yields 72.7 percent overlap when based on families of prey taken. Major types are also of the same relative importance when diets are compared on the basis of the number of individuals per taxon (Fig. 6).

Some interesting differences are noted when the taxa are considered on the basis of percent volume (Fig. 7). In both kingbirds, Orthoptera (almost exclusively acridid grasshoppers) are the largest constituent of the diet, despite their relatively less frequent occurrence and fewer numbers among prey items. The greater incidence of cicadas (Homoptera) in *vociferans* is probably related to the closer association of this species to riparian situations. However, it appears that this difference is accentuated in the volume comparisons because a greater proportion of the cicadas in *verticalis* samples had undergone extensive digestion. Kingbirds (*vociferans*) were only once observed feeding a dragonfly (Odonata) to nestlings; these insects were absent from all the stomach samples.

An unusual observation of a *vociferans* took place in the grassland-shrub,

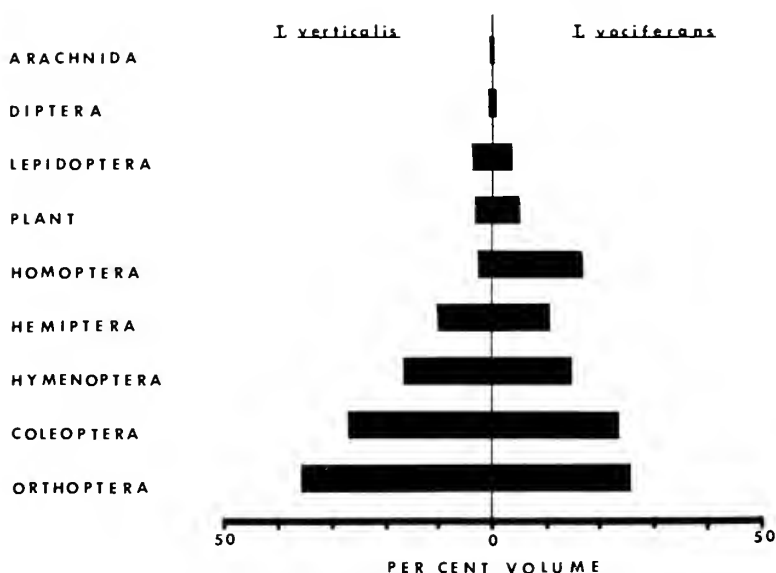


FIG. 7. Relative importance, expressed as percent total volume, of major prey types in *Tyrannus verticalis* (n = 48) and *T. vociferans* (n = 79) samples. Symmetry indicates similar diets of these birds.

west-southwest of Fort Davis, on 20 May 1970. There a bird flew down and caught a noticeably large prey item, which it abandoned as I approached. The prey was collected and later identified as a juvenile (5.5 g) harvest mouse (*Reithrodontomys* sp.). This was the only instance of predation on a vertebrate observed by me.

There were greater differences within samples of a kingbird species from the same locality on different dates and on the same date at different localities than within samples of both kingbird species at the same locality and date (Table 2). Admittedly, samples of the two species at the same locality were few, because generally they did not occur together. Even with meager data, interspecific comparisons are more appropriate than a strict seasonal analysis, because considerable bias could be introduced by the sampling methods (i.e. different times of day, habitat types, etc.). Some taxa occur regularly throughout the season (i.e. Acrididae, Reduviidae, Carabidae, Apoidea) while others are more temporal as well as local (as Dermestidae, Curculionidae, lepidopterous larvae, Formicidae).

AGONISTIC BEHAVIOR

Both species of kingbirds mobbed larger birds, including Red-tailed Hawks (*Buteo jamaicensis*), Great Horned Owls, and Common Ravens (*Corvus*

TABLE 2
 FOOD COMPOSITION (PERCENT OCCURRENCE) OF *TYRANUS VERTICILIS* AND *T. VOCEIFERANS*,
 INDICATING DIFFERENCES WITH LOCALITY AND TIME

| Prey taxa | <i>T. verticalis</i> | | | <i>T. verticalis/T. vociferans</i> | | | <i>T. vociferans</i> | | | |
|-------------------------------|---------------------------|---------------------------|----------------------------|------------------------------------|----------------------------|----------------------------|---------------------------|----------------------------|---------------------------|-----------|
| | Balmorhea | | | Plata | | | Plata | | | |
| | 26 May 1970 (n = 5) | 9 July 1970 (n = 6) | 27 Aug. 1969 (n = 5) | 10 June 1970 (n = 3) | 14 July 1970 (n = 2) | 17 Aug. 1970 (n = 1) | 18 May 1970 (n = 7) | 15 July 1970 (n = 8) | 28 May 1970 (n = 3) | Ash Creek |
| ORTHOPTERA | | | | | | | | | | |
| Acrididae | 3.6 | 13.6 | - | - / 7.1 | 20.0 / - | 33.3 / 18.8 | 7.1 | 6.2 | - | 10.7 |
| Undetermined | 3.6 | 4.5 | - | - / - | 20.0 / - | 33.3 / 18.8 | 7.1 | 6.2 | - | 7.1 |
| | - | 9.1 | - | - / 7.1 | - / - | - / - | - | - | - | 3.6 |
| HEMIPTERA | | | | | | | | | | |
| Belostomatidae | 21.5 | 27.2 | 7.2 | 9.1 / 14.2 | / | - / 18.8 | - | 6.3 | - | 28.6 |
| Nannorhidae | - | - | - | - / 7.1 | - / - | - / - | - | - | - | - |
| Reduviidae | 3.6 | 4.5 | 3.6 | 9.1 / - | - / - | - / - | - | - | - | - |
| Coreidae (<i>Mozona</i> sp.) | - | 18.2 | - | - / - | - / - | - / 12.5 | - | - | - | 14.3 |
| Corixidae | 3.6 | - | - | - / - | - / - | - / - | - | - | - | - |
| Pentatomidae | 14.3 | 4.5 | 3.6 | - / 7.1 | - / - | - / 6.3 | - | 6.3 | - | 10.7 |
| HOMOPTERA | | | | | | | | | | |
| Cicadidae | - | - | - | - / 14.3 | - / - | - / - | 14.3 | 37.5 | - | - |
| | - | - | - | - / 14.3 | - / - | - / - | 14.3 | 37.5 | - | - |
| COLEOPTERA | | | | | | | | | | |
| Circulididae | 49.9 | 18.0 | 64.2 | 54.6 / 49.9 | 20.0 / - | 33.3 / 37.7 | 7.1 | 6.2 | 15.4 | 39.3 |
| Carabidae | - | 4.5 | 17.8 | 9.1 / - | - / - | - / - | - | 6.2 | - | - |
| Hydrophilidae | 14.3 | 4.5 | 21.4 | - / - | - / - | - / 6.3 | - | - | - | 14.3 |
| Staphylinidae | - | - | - | 18.2 / 7.1 | / | - / - | - | - | - | - |
| Cantharidae | - | - | 21.4 | 18.2 / 21.4 | - / - | - / 6.3 | - | - | - | - |
| Dermestidae | 7.1 | - | - | - / - | - / - | - / 6.3 | - | - | - | - |
| Tenebrionidae (Adult) | - | 4.5 | - | - / - | - / - | - / - | - | - | - | - |

TABLE 2 (continued)

| Prey taxa | <i>T. verticalis</i> | | | <i>T. verticalis/T. vociferans</i> | | | <i>T. vociferans</i> | | | | | |
|-------------------------------------|----------------------|---------------------|----------------------|------------------------------------|--------------------------------|----------------------|----------------------|----------------------|---------------------|----------------------|----------------------|----------------------|
| | Balmorhea | | | Plata | | | Plata | | | Ash Creek | | |
| | 26 May 1970 (n = 5) | 9 July 1970 (n = 6) | 27 Aug. 1969 (n = 5) | 10 June 1970 (n = 4) | 14 July 1970 (n = 2/ n = 1) | 17 Aug. 1970 (n = 3) | 18 May 1970 (n = 7) | 15 July 1970 (n = 8) | 28 May 1969 (n = 3) | 28 July 1969 (n = 7) | 28 July 1969 (n = 3) | 28 July 1969 (n = 7) |
| COLEOPTERA (continued) | | | | | | | | | | | | |
| Tenebrionidae (Larva) | - | - | - | - | - | - | - | - | - | - | - | 7.7 |
| Scarabaeidae (<i>Phanaeus</i> sp.) | 3.6 | - | - | - | - | 33.3/12.5 | - | - | - | - | - | 25.0 |
| Chrysomelidae | 7.1 | - | - | 14.3 | - | - | - | - | - | - | - | - |
| Curculionidae | 17.8 | 4.5 | - | 9.1/ 7.1 | 20.0/- | - | 6.3 | 7.1 | - | - | - | - |
| Undetermined | - | - | 3.6 | - | - | - | - | - | - | - | - | 7.7 |
| LEPIDOPTERA | | | | | | | | | | | | |
| Pieridae (Adult) | - | 4.5 | 3.6 | - | - | - | 6.3 | - | - | - | - | 15.4 |
| Noctuidae (Adult) | - | - | - | - | - | - | - | - | - | - | - | 15.4 |
| Undetermined (Larva) | - | - | 3.6 | - | - | - | 6.3 | - | - | - | - | - |
| Undetermined (Adult) | - | 4.5 | - | - | - | - | - | - | - | - | - | - |
| DIPTERA | | | | | | | | | | | | |
| - | - | - | - | - | - | - | 6.3 | 7.1 | - | - | - | 15.4 |
| HYMENOPTERA | | | | | | | | | | | | |
| - | 21.4 | 31.7 | 38.6 | 36.4/14.2 | 60.0/100.0 | 33.3/12.5 | 42.9 | 43.8 | 30.8 | 10.7 | - | - |
| Chalcidoidea | - | - | 3.6 | - | - | - | - | - | - | - | - | - |
| Scolioidea | 3.6 | 4.5 | - | - | - | - | - | - | - | - | - | 7.7 |
| Formicidae | - | 9.1 | 17.8 | 18.2/ 7.1 | 40.0/100.0 | - | - | 31.3 | - | 10.7 | - | - |
| Vespidae | - | 4.5 | 3.6 | - | - | - | - | - | - | - | - | - |
| Apioidea | 17.8 | 13.6 | 13.6 | 18.2/ 7.1 | 20.0/- | 33.3/12.5 | 42.9 | 12.5 | 23.1 | - | - | - |
| TOTAL INSECTA | | | | | | | | | | | | |
| - | 96.4 | 95.0 | 100.0 | 100.1/99.7 | 100.0/100.0 | 99.9/100.4 | 78.5 | 100.0 | 77.0 | 89.3 | - | - |
| SOLPUGIDA | | | | | | | | | | | | |
| Solpugidae | - | - | - | - | - | - | - | - | - | - | - | 7.7 |
| ARANEIDA | | | | | | | | | | | | |
| Thomisidae | 3.6 | 4.5 | - | - | - | - | - | - | - | - | - | - |
| SEEDS (Anacardiaceae) | - | - | - | - | - | - | 21.4 | - | 15.3 | 10.7 | - | - |

corax). Such attacks were made simultaneously by the two species on an owl (and the stuffed decoy) and also on two ravens at Plata. A Boat-tailed Grackle (*Cassidix mexicanus*), which entered their nest tree, was harassed simultaneously by a *verticalis* and a Scissor-tailed Flycatcher (*Muscivora forficata*). Such aggressive behavior has obvious selective value in protecting eggs and nestlings from predation, as well as in defense against birds which might utilize the nest materials for their own nest construction.

Intraspecific territoriality in *verticalis* was frequent, especially in the birds nesting near each other at isolated localities of favorable habitat. At Plata a pair, which began nesting earlier than two others, dominated the area, excluding all other *verticalis*. One of the other two pairs eventually nested in a tree 180 ft away, but the third pair never constructed a nest—although at times the birds behaved as though they had selected a nest site.

Verticalis/vociferans interactions were observed near Plata, where a *verticalis* chased a *vociferans* from near the former's nest, but the *vociferans* returned. *Vociferans* were tolerated when they approached other *verticalis* nests; however, at a nearby locality a *verticalis* was chased by a nesting *vociferans*. The latter's nest had been partly dislodged by a strong wind the preceding evening, and earlier in the day the *verticalis* had taken nest material from it for their own construction. When not near their nests, the two species often perched within ten feet of each other and fed without interaction from the same perches.

Intergeneric aggression between *verticalis* and *Muscivora forficata* was observed on four occasions. In each instance it occurred near the nest of one of the birds, with defense manifested only in the immediate nesting area (i.e. less than 100 ft). At one such locality the birds subsequently constructed nests that were separated by a distance of only 30 ft, compared to two *verticalis* nests there separated by 195 ft. Away from their nest sites, *verticalis* and *M. forficata* were observed feeding together without aggression, and on some occasions they were perched within four ft of each other. Because of similarities in behavior and the occurrence of an intergeneric hybrid, Davis and Webster (1970) support the proposal of Smith (1966) to include *M. forficata* in the genus *Tyrannus*.

When near their nests, *verticalis* showed aggressive behavior toward a Say's Phoebe (*Sayornis saya*), a Vermilion Flycatcher (*Pyrocephalus rubinus*), and House Sparrows (*Passer domesticus*). The phoebe was attacked when as much as 20 ft away, while the other two species were allowed closer to the *verticalis* nests. An Ash-throated Flycatcher (*Myiarchus cinerascens*) was not given any apparent attention by *verticalis*, even when on two occasions it perched ten ft from their nest. Also ignored were Brown-headed Cowbirds (*Molothrus ater*), which came as close as three ft from perched kingbirds.

Intraspecific aggression by *vociferans* was observed only on two occasions. However, when near nests, *vociferans* several times attacked Cactus Wrens (*Campylorhynchus brunneicapillus*) and once each House Finches (*Carduelis mexicanus*) and *T. verticalis*. An Orchard Oriole (*Icterus spurius*) was tolerated at five ft from a nest and a Vermilion Flycatcher at three ft. Nesting *vociferans* and *Muscivora forficata* occurred within 100 ft of each other, although the latter species tended to occur more frequently in habitats occupied by *verticalis* than by *vociferans*.

DISCUSSION AND CONCLUSIONS

Theoretically, species such as *T. verticalis* and *T. vociferans* can coexist only if each inhibits increase of its own population more than it does the other's (MacArthur, 1958). The most productive approach in studies of the ecological and other relationships of sympatric species is examination of the ways in which the resources of an area are used. Using this approach, I considered three principal aspects: utilization of different resources, of the same resources at different places, and of the same resources in different ways. If species are so different that mutual exclusion does not provide any increased access to a limited resource, interspecific aggression should, in time, decrease or disappear (Orians and Willson, 1964).

In the two breeding *Tyrannus* species in the Trans-Pecos, i.e. *verticalis* and *vociferans*, I did not find any interspecific defense of feeding areas, but such behavior was manifested in relation to nesting sites. This suggests that nesting sites are the resource most limited in supply and therefore worthy of defense. A large part of potential competition for nest sites is avoided through the distinct altitudinal segregation of the kingbirds throughout most of the region. Eighty-three percent of the *verticalis* nests were at elevations less than 4,000 ft, compared to 83 percent of those of *vociferans* at elevations in excess of 4,000 ft. None of the *verticalis* nests were at elevations greater than 4,500 ft and only one *vociferans* nest was found below 3,500 ft. This altitudinal segregation translated into difference in the habitat types used by the species. Thus, pine-oak-juniper, grassland, and riparian types were dominated by *vociferans*, whereas *verticalis* predominated in the desert shrub and farmland types.

Both species nested on man-made structures, but *verticalis* did so to a greater extent—as befits its occupancy of more open situations. Trees were preferred by both species for nesting, with *verticalis* nests lower (relatively and absolutely) than *vociferans*. This was not true in Arizona, where Hespensheide (1964) found these two species nesting in the same portions of trees. There only trees and shrubs were used and the birds were relatively more abundant than in the Trans-Pecos.

There were greater differences in the food taken by a species at a locality on different dates than by the two species at a locality on the same date. The extent of overlap in diets was 72.7 percent in families of insects and other prey taxa, but was complete in groups such as orders.

Other potential competitors of kingbirds include several species of flycatchers and non-flycatchers. The Scissor-tailed Flycatcher is biologically similar to the *Tyrannus*, occurring sympatrically with both, but more frequently with *verticalis*. An instance of interspecific aggression was observed between these two species, perhaps leading to their subsequent nesting in adjacent, rather than the same, trees. The hole-nesting Ash-throated Flycatcher occurs throughout much of the region, but it did not compete with either species in this study. Other species of flycatchers (e.g. *Sayornis* spp.) occur so infrequently that they have no obvious effect on the populations of the species studied.

Such species as the Loggerhead Shrike (*Lanius ludovicianus*) and the Mississippi Kite (*Ictinia mississippiensis*) take some of the same foods as the kingbirds but are sufficiently different otherwise in their biology that they are not obviously competitors.

SUMMARY

The kingbirds *Tyrannus verticalis* and *T. vociferans* were studied for possible competitive relationships in the Trans-Pecos region of Texas during June–August 1969 and May–August 1970, with supplemental observations in November 1970 and May 1971. The geographical and ecological distribution, nesting habits, food composition, and behavioral interactions were examined in each species.

Although the kingbirds were geographically sympatric, *verticalis* generally occupied elevations of less than 4,000 ft and *vociferans* predominated above 4,000 ft. Desert shrub and farmland were typically occupied by *verticalis*, whereas *vociferans* was more abundant in the pine-oak-juniper, grassland, and riparian habitats. Both species preferred trees as a nesting substrate, but *verticalis* often nested on man-made structures such as utility poles in open habitat where trees were not commonly found. Despite their occurrence in different habitat types, the kingbirds fed in a similar manner and had similar diets. There was no apparent interspecific defense of feeding areas, although the nest sites were defended.

ACKNOWLEDGMENTS

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KIRTLAND'S WARBLER AND ITS BAHAMA WINTERING GROUNDS

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The Kirtland's Warbler (*Dendroica kirtlandii*) has an extremely limited range, breeding solely in central Michigan and wintering only in the Bahama Islands. In addition, this warbler is a genuinely endangered species, with a total population that has declined from perhaps 1,000 individuals in 1951 and 1961 (Mayfield 1953, 1962) to about 400 in 1971-1973 (Mayfield, 1972a, 1973a, 1973b). The decline in the species in the last 10 to 20 years is certainly real, and factors most likely involved in it are: 1, the probably adverse effect of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*); 2, a possibly inadequate amount of suitable breeding habitat; 3, a possible worsening of conditions on the wintering grounds in the Bahama Islands.

The first two factors are receiving adequate attention, at least judging from my experiences since becoming involved with the species in 1961. Consequently, I have concentrated on the third factor, as I recently had the good fortune of spending some time in the Bahamas. The following is a report on that venture.

WINTER RECORDS OF THE KIRTLAND'S WARBLER

The first clue that the Bahama Islands constituted the winter range of the Kirtland's Warbler came when a female was collected on Andros Island in 1879 (Cory, 1879). All winter records since then have been restricted to the Bahamas, and Van Tyne (1951, including map p. 540—also in Mayfield, 1960:38) gave a total of 71 specimens having been collected there. Of these, 66 were taken in the 14 year period, 1884-1897. After 1897, collections (and reliable sight records) dropped almost to the vanishing point.

In 1902 a specimen was collected on New Providence and another on Little Abaco (Bonhote, 1903). Maynard collected one on New Providence in 1913 and (possibly) another on the same island in 1915 (Van Tyne, 1951). A final specimen was taken on San Salvador (Watlings) in 1965 by Paulson (Mayfield, 1972b).

Van Tyne (1951) reported a sighting of a Kirtland's Warbler on Great Inagua by James Bond sometime in the period 1935-1940. Hundley (1967) lists the sighting of three on New Providence by Street in 1941. Challinor (1962) saw one on Hog Island (since renamed Paradise Island) in 1957. Since 1959 there has been a steady trickling of sightings on Grand Bahama, by groups from the Florida Audubon Society. From 1959 through 1966 they

sighted 13 Kirtland's Warblers on Grand Bahama, as well as two on Eleuthera (Hundley, 1967). Andrew Paterson (pers. comm.) saw three on Andros during a 3½ year residence ending in May 1971. Dr. John T. Emlen, Jr. (pers. comm.) saw one on Andros in 1970. Dr. Paul Fluck has observed at least five on Grand Bahama since taking up residence there in 1969. Fluck caught two of these in mist nets and banded them. To my knowledge he is the only person to have banded this species on its wintering grounds.

It seems obvious that the species was considerably more numerous in the 1880's and 1890's—as inferred from the collections in the Bahamas. It is thought that the population rose in that period in response to an increase in habitat. This was brought about by the forest fires which followed the lumbering operations in Michigan, which were at their height in the period 1875–1900. Furthermore, perhaps this increase was relatively unhindered by cowbird parasitism, as possibly this species did not build up to peak numbers on the Kirtland's Warbler nesting range until about 1900 (Mayfield, 1960:35, 1961).

Then winter records dropped off in this century apparently because there were fewer birds to be seen. This reduction coincides with the reduction in habitat—concomitant with increasingly effective fire fighting techniques—and, probably more importantly, with the maximizing of cowbird numbers.

MATERIALS AND METHODS

In 1972 I was in the Bahamas from 8 February to 13 April, visiting: Grand Bahama, Abaco, Andros, Eleuthera, and New Providence. In 1973 I was there from 6 January to 3 April, visiting: Exuma, Long Island, San Salvador, Cat Island, Crooked Island, and Acklins Island. The purposes of my visits were much the same in both years: 1, to survey and assess recent habitat changes; 2, to find Kirtland's Warblers, if possible; 3, to try to determine what the warbler's requirements are in winter and correlate these with findings regarding observed habitat changes.

On each island I used a car for convenience in traveling the main roads. I surveyed, on foot, all trails, secondary vehicular roads, and many areas with no trails, for as long as my schedule permitted on each island. Combining the two years, I spent 800 hours in the field.

This routine provided good opportunity for a fairly extensive observation of habitats and habitat changes. The chances of seeing a Kirtland's Warbler this way are extremely small. To help increase the odds somewhat, I used a tape recorder (a Uher 4000L) for play-back of species song. The feasibility of this method was presented by Gorski (1969, 1972) for another species.

A SIGHTING ON CROOKED ISLAND

During my 800 hours of field work, I sighted only one Kirtland's Warbler: a male seen toward the east end of Crooked Island, southern Bahamas. I observed what I believe to be the same male (see reasons below) during three different days, spanning a period of 12 days: 11, 12, and 22 March. I saw

him from as close as two meters (and with binoculars), with actual observations totaling just under two hours during the three days. He appeared to be in complete breeding plumage except for a slight molting on the chin. The central part of his breast was immaculate, and I assumed from this that he was a fully adult male. He had an asymmetrical black blotch on the left side of his upper breast—this being the basis for my assumption that the same male was involved in all observations. This brings to 16 the number of islands and cays in the Bahamas on which Kirtland's Warblers have been collected (11) or reliably sighted.

I initially located this male Kirtland's Warbler through his responses to my playing recorded songs of the species. Essentially, these responses consisted of rather loud and persistent chipping and an approach towards the recorder. After the male was in sight, I did not play the recorder further. Rather, I turned it off and tried to follow him for as long as possible while his excitement subsided and he resumed his routine. After he was lost to view for some minutes, I played two or three songs only, to reestablish contact.

His reaction to recorded song on 12 March was similar to, but weaker than, his reaction on the previous day. He was not sighted on 13 or 14 March, although I walked about the area playing groups of five or six songs intermittently. On 15 March I proceeded to Acklins Island, as previously planned. I went back to Crooked Island on 21 March and returned to the warbler area on 22 March. On that day the male responded to play-back of song, although at the weakest level yet.

The territory or "foraging area" (term suggested by Harold Mayfield, pers. comm.) occupied by this male may well have been larger than I allowed for, although I played well outside the relatively small area wherein he was actually observed. This observation area measured just under 0.5 hectare. Considering the length of time it sometimes took him to respond, the direction from which he came, and the approximate distance the recorded song penetrated the scrub (about 200 m), a *guess* would be that he utilized at least seven ha (about 17 acres). The lack of responses on 13 and 14 March suggests the possibility of an even larger area. Alternatively, the lack of response may represent habituation to the recorded song as suggested, for somewhat different circumstances, by Emlen (1969).

After 22 March I could not find the male warbler again, although I tried on four other days through 31 March. I suspect that was *about* the time for him to begin northward migration. There are only four records from the southern Bahamas, two from the Caicos in January or February 1891, Bond's sighting on Inagua on 8 March, and the Crooked Island male as late as 22 March. All April Bahamian records are from farther north.

Behavior.—Some of the records submitted by Hundley (1967) on Grand Bahama involved observations of Kirtland's Warblers moving up the trunks of mature Caribbean pines (*Pinus caribaea*), in the manner of the Brown Creeper (*Certhia familiaris*). As Hundley points out, this behavior has not been observed on the breeding grounds, not did I see it in the male on Crooked Island. However, the trees on the Crooked Island foraging area were much smaller—up to only about 10 cm dbh—than those on Grand Bahama.

Of the time the Crooked Island male was observed in ordinary activities (i.e., not interfered with by the recorded song), about 70 percent was spent on the ground, actively hunting for food. While trade winds were not unusually strong during these observations, perhaps 8–16 knots, the bulk of the small insects may still have been near the ground. No food items were identified, but judging from the maneuverings of the male, the food items were not stationary. All items taken were small (presumably insects and spiders). Cory (1879) reported the stomach contents of the Andros female as "insects."

Avian associates.—The foraging area was not rich in bird life. Only 16 other species were noted during nine days (11 to 14, 22, 26, 28, and 30 to 31 March): Osprey (*Pandion haliaetus*), Peregrine Falcon (*Falco peregrinus*), Zenaida Dove (*Zenaida aurita*), Common Ground Dove (*Columbina passerina*), Bahama Woodstar (*Calliphlox evelynae*), Gray Kingbird (*Tyrannus dominicensis*), Bahama Mockingbird (*Mimus gundlachii*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Thick-billed Vireo (*Vireo crassirostris*), Black and White Warbler (*Mniotilta varia*), Yellow Warbler (*Dendroica petechia*), Prairie Warbler (*D. discolor*), Palm Warbler (*D. palmarum*), Bananaquit (*Coereba flaveola*), Stripe-headed Tanager (*Spindalis zena*), and Black-faced Grassquit (*Tiaris bicolor*).

The Osprey(s) and falcon(s) were passing overhead. The other species, each observed on almost every visit to the area, had a greater potential of being in close association with the Kirtland's Warbler. No conflicts—or even close approaches—were observed between the male Kirtland's Warbler and any other bird.

Habitat.—The dominant plant (vernacular names supplied by Mr. and Mrs. G. Ferguson—see Acknowledgments—and scientific names from Britton and Millspaugh, 1920) on the foraging area was "buttonwood." Both "black buttonwood" (probably black mangrove, *Avicennia nitida*) and "white buttonwood" (*Conocarpus erectus*) were present, with the former in greater abundance. Some of the other plants on the area were: "brasiletto" (*Caesalpinia* sp.), "cat's-paw" (*Solanum didymacanthum*), "madeira" (*Swietenia mahagoni*), "poisonwood" (*Metopium toxiferum*), "Lucy bush," "cherry,"

"marginelee," "wild plum," "rock bush," "darlin plant," "serfean," and "spoon bush." There were also two species of cactus: "dildo" (*Cephalocereus* sp.), and *Opuntia* sp. No plant, such as century-plant (*Agave* spp.), with a profusion of blossoms serving as a "food center" for both nectar- and insect-feeding birds, was present.

The dominant ground cover, of interest because the male Kirtland's Warbler spent so much time on or near the ground, was Bermuda grass (*Capriola dactylon*). There were lesser amounts of "parsley" and "broom." There was also much exposed limestone rock.

The habitat had somewhat the same configuration as do the jack pine (*P. banksiana*) areas on a typical, optimal breeding territory, i.e., there were thickets and openings. By "squinting," one could visualize the "habitat gestalt" much as it appears in Michigan (the shrubbery on Crooked Island is, of course, broad-leaved). The general height of the shrubbery was 1 to 1½ m. with a scattering of taller plants to a height of about 6 m.

On the larger Bahamian islands, the land often rises away from the sea to form a coastal ridge. Immediately inland from this ridge there is often a lower area or trough. Still farther inland from the trough the land more or less gradually rises to form the main part of the island. Depending on the depth of the trough, as well as on other factors, the habitat in this low area is variously marsh, mangrove swamp, pond, or a rather dry area—often dominated by coconut palm (*Cocos nucifera*) or thatch palm (*Thrinax* sp.). Existing water in the trough is brackish and the levels often rise and fall with the tides.

The area on which I found the male warbler was about 900 m north of the sea. The trough behind the coastal ridge (a very low, broken ridge in this instance) was occupied by a mangrove (*Rhizophora mangle*) swamp. The elevation inland from the mangrove increased only gradually. Thus as one proceeded inland from the mangrove one found, successively: a zone of stunted and very sparsely scattered mangrove; a zone consisting almost entirely of bare rock and Bermuda grass; a zone of stunted shrubland in which the Kirtland's Warbler was located; and, finally, the taller scrub typical of many of the southern Bahama islands.

The plants on the area occupied by the Kirtland's Warbler occur on, as it were, an intermediate zone—in both elevation and salinity of ground water. The stunted habit is perhaps due to the ground water being brackish. One dominant plant on the area (the probable black mangrove) evidenced these conditions (and its adaptation to them) by its large size and relative abundance (and by its ability to exude salt through its leaves). Most of the other plants on the area are also found farther inland, and existence in this inter-

mediate zone appears to be marginal for them. They were not only stunted but less densely distributed than is the case only slightly farther inland.

Such an intermediate zone can be found along many stretches of coast and around the perimeters of many inland low areas. These zones are narrow—as narrow as 200 m—and would constitute a rather severe restriction of distribution and habitat choice for any organism limited to them. We have no evidence that the Kirtland's Warbler is so restricted. Also we have no way of knowing yet how typical this male might be relative to others of the species utilizing non-pine areas and islands in winter.

Such areas as the above appear in no imminent danger as they are not in demand by man. Island farming would be impossible in such areas. Any coastal area is in *potential* danger of alteration through highway construction and coastal development in general.

ENVIRONMENTAL CONDITIONS IN THE BAHAMAS

Lumbering of Caribbean pine forest.—The most significant environmental alteration I observed—and probably the most significant single change ever to occur in the Bahamas—was the lumbering of the Caribbean pines. To my knowledge, only four islands support pines: Grand Bahama, Abaco, New Providence, and Andros. Britton and Millspaugh (1920) state that this pine species is also found in the Caicos, but I have not visited these islands nor found evidence to verify this. There are no pines on the western end of Grand Bahama. They begin about five or six km west of Freeport and cover much of the remainder of the island eastward.

The Abaco Lumber Company carried on a pulpwood operation on Grand Bahama from about 1948 to 1955. From 1956 to 1959, Owens-Illinois also engaged in a pulpwood operation on Grand Bahama. They lumbered off some 53,000 ha (130,000 acres). (The total area of Grand Bahama is about 111,000 ha or 275,000 acres.) They then moved to Abaco, lumbering there until 1970, and in 1968, they began on Andros. They were cutting on Andros when I was there in March 1972, and my impression is that they were to be done there by the end of 1973.

In this 18 year period, from 1956 to 1973, Owens-Illinois has used a 10 cm (4 inch) dbh criterion—i.e., all trees 10 cm dbh and over were cut. Five "seed trees" per acre were left standing for regeneration. Regeneration on Grand Bahama has been good. On Abaco, recurrent forest fires have stalled regeneration on a large area in the south, where an approximate 20,000 ha (55,000 acre) area is now virtually treeless. Most of the rest of Abaco has also been lumbered, and regeneration northward seems good. The total area of Abaco is about 168,000 ha (415,000 acres). It is still too early to judge the quality of pine regeneration on Andros. Caribbean pines are slow-

growing, and the establishment of young pines is constantly threatened by forest fires (particularly in the drier, winter months). I observed unattended (and unfought) forest fires burning for days on both Grand Bahama and Andros.

The pulpwood operations at least temporarily remove, and sometimes completely destroy, the Caribbean pine association or ecosystem over vast areas on the islands involved. The recent Kirtland's Warbler sightings on Grand Bahama (Hundley, 1967) among Caribbean pines suggest that some portion of the population utilizes this habitat in winter. Warblers have, in fact, been observed on both the pines proper and on the broad-leaved plants of the understory. It makes little difference what kind of plant they use at any given moment in these areas, as the entire association to which they are attracted, and upon which they depend, is being severely affected by the pulpwood operation. To the extent that the Kirtland's Warbler, as a species, relies on pinelands in winter, lumbering could well have been detrimental to the point of having contributed to the recent decline in their numbers.

Usage of scrub habitats.—Most of the winter records of Kirtland's Warbler are from the northern Bahamas. It seems inescapable that this is true simply because there are more visitors to these islands. For example, 45 of the 72 specimens have been collected from New Providence, where ships have been putting in for decades. The four "pine islands" are also in the north. However, even there many of the Kirtland's collected or seen have been in broad-leaved scrub. More telling, it would seem, is the fact that 24 specimens have been taken on islands and cays which lack pines.

Unfortunately, collectors reported very little regarding the habitats in which the warblers were taken. Thus, while one might wish the literature contained much more information on this aspect, one is forced to the same conclusion Mayfield (1972b) drew from the available data: "The Kirtland's Warbler usually inhabits low, broad-leaved scrub in the Bahamas. Areas that have been cleared and then allowed to grow back but have not yet reached their maximum height and density . . . it is significant that no one has reported them in the high scrub or coppice, trees 15 feet or more in height, that abound in these islands."

I agree especially with the possible significance to the warbler of the small scrub size: however, such areas do not have to begin with cleared land. New Providence, and particularly Nassau, have been fairly heavily populated for a long time. Much of the land there must have been cleared for agriculture and then variously abandoned. Such a circumstance might have attracted a greater number of Kirtland's to these areas. It is even possible that the greater number of Kirtland's Warblers collected on New Providence is not entirely an artifact of the presence of a greater number of collectors: this

may, in part, result from ideal habitat conditions and a concomitant higher local warbler population.

Such clearing of the land has not been nearly so extensive on the Out Islands, with the possible exception of Eleuthera. Certainly it was not true in the past when the Kirtland's Warblers were wintering in the Bahamas, long before the Arawak Indians settled there. Rather, a supply of this low scrub habitat could result from the stunted growth described earlier. It is likely that such areas have always existed in the Bahamas. In fact, judging from the extensive shallow offshore areas of today, such stunted areas were probably greater in extent during glacial maxima when sea levels dropped, exposing more land of very low altitude.

While an unknown proportion of the total Kirtland's Warbler population utilized the Caribbean pine ecosystem in winter (this proportion likely varied from year to year), from at least spatial considerations, it appears that the bulk of the population is to be found in low, broad-leaf scrub growth—either young or stunted. If so, this would narrow down the search area for them somewhat. Hopefully enough careful records can be obtained in the next few years to permit a fairly definitive statement on the winter requirements of this species.

Other possibilities.—Another possibility exists as a contributing factor to the recent Kirtland's Warbler decline and should be stated here. Both Paul Fluck, in the Freeport, Grand Bahama, area, and Alexander Sprunt, in Tavernier, Florida, report heavy losses among various species of warblers during spring migration of 1971. Both believe that the drought conditions that prevailed during much of the winter of 1970–1971 in the Bahamas and southern Florida were responsible. Presumably the drought reduced the insect populations, and many warblers may have starved in a time of high energy needs. It is impossible to put these losses in numerical terms. However, Fluck described the warbler losses on Grand Bahama as very heavy, with “bushel baskets” of dead birds along the Queen's Highway every morning. We know nothing about the distribution in time of the 60 percent decline of the Kirtland's Warbler between 1961 and 1971; however, a catastrophic type loss cannot be ruled out as a partial cause.

SUMMARY

The population of Kirtland's Warbler declined from an estimated 1,000 in 1961 to about 400 in 1971. Principle causes appear to be parasitism by the Brown-headed Cowbird and a possibly inadequate amount of breeding habitat. The species requirements on its wintering grounds in the Bahama Islands are virtually unknown. Necessary conditions there may be worsening.

Most of the winter records of Kirtland's Warbler are reviewed. I spent 800 hours in the field on 11 of the larger islands during the winters of 1971–1972 and 1972–1973,

trying to find Kirtland's Warblers by means of recorded song, and surveying habitats and recent habitat changes. One male Kirtland's was seen on Crooked Island. The bird was under observation for just under two hours during three days—11, 12, and 22 March 1973. It occupied an area perhaps twice the size of an average breeding territory. This area consisted of low, broad-leaved scrub with a stunted habit, possibly due to the brackish ground water. The plants on this foraging area are described in some detail.

The most profound habitat change observed has been the lumbering off of the Caribbean pines by the Owens-Illinois Company on the "pine islands" of Grand Bahama, Abaco, and Andros between 1956 and 1973. This destruction of the pine ecosystem may well have contributed to the recent decline in the Kirtland's Warbler population. It may be, however, that most of the population utilizes young or stunted broad-leaved scrub areas in winter. The proportions are unknown. A drought in the Bahamas and southern Florida in the winter of 1970-1971 may have led to the observed heavy loss of birds in the spring migration of 1971. This, too, may have contributed to the Kirtland's Warbler decline.

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28 STATE STREET, HILLSDALE, MICHIGAN 49242. ACCEPTED 25 FEBRUARY 1974.

THIRD NATIONAL WILD TURKEY SYMPOSIUM

This symposium will be held at San Antonio, Texas, on 11-13 February 1975, under the sponsorship of the Texas Chapter of the Wildlife Society. The theme is "The Wild Turkey: Its restoration, preservation, and management." Formal papers are slated for the first two days, and a full roster of speakers has been recruited from universities, conservation agencies, and elsewhere. The symposium will be at the Sheraton San Antonio Motor Inn, and information can be obtained on the event from Mr. Charles W. Ramsey, Wildlife Extension Specialist, Wildlife and Fisheries Dept., Texas A & M University, College Station, Texas 77843.

DOMESTIC CATS AS PREDATORS AND FACTORS IN WINTER SHORTAGES OF RAPTOR PREY

WILLIAM G. GEORGE

The domestic cat (*Felis catus*) was introduced into the United States over 150 years ago. Imported in small numbers for the primary purpose of controlling rodents in our eastern seaboard cities, cats remained scarce for many years. Now an estimated 31 million cats exist across the country (American Humane Association, 1972), and rural cats probably rival in numbers all other large predators combined east of the Great Plains, west of the Sierra Nevada, and in various other localities. In terms of impact on the avifauna, cats may pose little direct threat, for they are reported to kill relatively few birds in most situations (Table 1). Yet as predators on rodents, cats inevitably compete for prey with many of our declining raptors, and therein may lie a serious problem.

Cats are formidable competitors, able to kill rodents at a great and rapid rate. For example, the removal in eight months of over 4200 mice from a 35-acre study plot was ascribed principally to six cats by Pearson (1964). I am not suggesting a cause-and-effect relationship exists between the historical increase of cats and the historical decrease of raptors; however, cats, which are as efficient in their way as guns and DDT, accompany and add another dimension to man's encroachment into wildlife areas. The effects of cat abundance in and about wildlife areas should be monitored as a matter of prudence, especially in view of the decline (see Arbib, 1972) of such formerly "common" raptors as the Red-shouldered Hawk (*Buteo lineatus*), Red-tailed Hawk (*B. jamaicensis*), Marsh Hawk (*Circus cyaneus*), and American Kestrel (*Falco sparverius*), each of which feeds on rodents to a marked degree (May, 1935; MacAtee, 1935).

Most environments in rural America have suffered drastic and repeated alterations; many may be unable today to generate prey in sufficient densities to sustain both raptors and significant numbers of cats. I decided to probe this possibility when a female cat and two of her offspring killed an impressive number of mammals at my home in southern Illinois. I have studied continuously the predation by these cats over the past six years. During this time, shortages in the mammalian prey of hawks have appeared consistently in the cats' hunting grounds each winter. The present report describes and discusses the annual and seasonal predation by these cats from 1 January 1968 through 31 December 1971. Their predation on non-mammalian vertebrates (various birds, reptiles, and frogs) is tabulated to round out the account.

TABLE 1

FREQUENCY OF OCCURRENCE OF VERTEBRATE PREY IN THE DIET OF RURAL CATS¹

| Area | Percent or relative proportion of prey in each group | | | | | |
|---------------------------|--|---------|---------|-------|----------|------------|
| | Shrews-moles | Rodents | Rabbits | Birds | Reptiles | Amphibians |
| Maryland ² | 8 | 65 | 12 | 14 | — | — |
| Pennsylvania ² | 9 | 60 | 18 | 13 | — | — |
| Wisconsin ² | 2 | 82 | 5 | 11 | — | — |
| Michigan ³ | 0.9 | 95.9 | 0.2 | 3 | — | — |
| Ontario ³ | Few | Many | — | Few | — | — |
| Missouri ² | 4 | 68 | 12 | 10 | 5 | 1 |
| Oklahoma ² | Few | Many | Many | Few | Few | Few |
| Texas ² | — | 65 | 11 | 11 | 13 | — |
| California ² | — | 71 | 8 | 20 | — | — |

¹ Compiled from Bradt, 1949; Eberhard, 1954; Errington, 1936; Hubbs, 1951; Korschgen, 1957; Llewellyn and Uhler, 1952; McMurry and Sperry, 1941; Parmalee, 1953; and Toner, 1956.

² Based on analysis of stomach contents.

³ Based on observed predation.

MATERIALS AND METHODS

The Study Site.—The hunting grounds of the cats centered around our home in fallow farmland near the village of Cobden, Union County, southern Illinois. The area is one of uplands, known as the Shawnee Hills or Illinois Ozarks, which run east to west between the floodplains of the Mississippi and Ohio Rivers. This rolling country was once dominated by forest but now hosts orchards, cultivated crops, old field succession, pastures, second-growth deciduous woods, and impoundments that at many points intercept the natural watersheds.

Characteristically, the area is dotted with small farms, of which my home plot (in 11S, R, 1W, Section 19, Union County) is typical. The house stands atop a knoll, 0.3 mi from the nearest surfaced road and dwelling of a neighbor. An acre of lawn and an aged grove of conifers (*Tsuga*, *Pinus*, *Juniperus*) and deciduous hardwoods (*Quercus*, *Fraxinus*, *Acer*, *Juglans*, *Carya*, *Liquidambar*, *Liriodendron*) surround the house; a barn is close-by. Apple and nectarine (*Pyrus*) orchards (about 50 acres), old fields (25 acres), woods (15 acres), and several impoundments compose the adjacent habitats.

Ground cover in the fields and orchards agree in general composition but differ in height, as a result of differential mowing. In 1968–1971, annual and sometimes biannual mowing occurred on about 75 percent of the total field and orchard acreage. The woods on the plot skirt the fields; one forest-like stretch extends up a ravine to within a few feet of the barn.

The Mammalian Fauna.—The three cats had merely to step out of the barn or off the lawn to enter habitats containing 18 species of possible mammalian prey (Table 2), including three microtines, seven other rodents, three shrews, and the cottontail. Observations, a program of can-trapping for shrews (George, MS), and specimens caught by the cats indicated the summer abundance of these species approximated that reported by Hoffmeister and Mohr (1957) and Layne (1958), shown in Table 2.

TABLE 2
OCCURRENCE AND SUMMER ABUNDANCE OF SMALL TERRESTRIAL MAMMALS (EXCLUDING CARNIVORES) AND THEIR STATUS AS PREY OF WINTERING HAWKS NEAR COBDEN, UNION COUNTY, SOUTHERN ILLINOIS

| Species | Summer abundance ¹ | Winter status as prey for ² | | |
|---|-------------------------------|--|------------|------------------|
| | | Red-tailed Hawk | Marsh Hawk | American Kestrel |
| Opossum (<i>Didelphis marsupialis</i>) ³ | C | n | n | n |
| Eastern mole (<i>Scalopus aquaticus</i>) | VC | b | b | b |
| Long-nosed shrew (<i>Sorex longirostris</i>) ⁴ | U | n | n | n |
| Short-tailed shrew (<i>Blarina brevicauda</i>) | VC | b | b | a |
| Least shrew (<i>Cryptotis parva</i>) ⁵ | C | n | n | b or n |
| Woodchuck (<i>Marmota monax</i>) ⁶ | C | n | n | n |
| Eastern chipmunk (<i>Tamias striatus</i>) ⁶ | C | n | n | n |
| Eastern gray squirrel (<i>Sciurus carolinensis</i>) | U | a or b | b | n |
| Eastern fox squirrel (<i>Sciurus niger</i>) | U | a or b | n | n |
| Southern flying squirrel (<i>Glaucomys volans</i>) ³ | U | n | n | n |
| White-footed mouse (<i>Peromyscus leucopus</i>) ³ | VC | b | b | b |
| Southern bog lemming (<i>Synaptomys cooperi</i>) | U | b | b | b |
| Prairie vole (<i>Microtus ochrogaster</i>) | VC | a | a | a |
| Pine vole (<i>Microtus pinetorum</i>) | C | a | a or b | a or b |
| Muskrat (<i>Ondatra zibethicus</i>) | U | b or n | n | n |
| House mouse (<i>Mus musculus</i>) | C | b | a or b | a |
| Meadow jumping mouse (<i>Zapus hudsonius</i>) ^{3, 6} | U | n | n | n |
| Eastern cottontail (<i>Sylvilagus floridanus</i>) | VC | a | b | n |

¹ VC = very common, C = common, U = uncommon.

² a = major, b = minor, n = negligible.

³ Strongly crepuscular-nocturnal.

⁴ Rare in most of southern Illinois.

⁵ Taken frequently by owls but seemingly not often by hawks.

⁶ Winter hibernator.

Non-feline Predators.—The study plot was ranged over by the following native predators, which, to a greater or lesser extent, competed with the cats for prey the year round (except as noted): various snakes (winter hibernators), Red-tailed Hawk, Marsh Hawk (winter visitant), American Kestrel, Screech Owl (*Otus asio*), Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Long-eared Owl (*Asio otus*; winter visitant), Loggerhead Shrike (*Lanius ludovicianus*), raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes fulva*), domestic dog (*Canis familiaris*), and perhaps striped skunk (*Mephitis mephitis*). The long-tailed weasel (*Mustela frenata*) and mink (*M. vison*) have been recorded in nearby areas but not on the study site, and evidence is lacking to show that short-tailed shrews, which elsewhere may kill voles, prey on microtines in southern Illinois.

Human predation existed in the form of sportsmen, who annually harvested gray and fox squirrels (1 August to 15 November) and cottontails (11 November to 15 January) within all but the inner core (six acres) of the study plot. A minor amount of trapping was done by me to study the composition of the small mammal fauna, but neither rodent control nor a chemical eradication program was in effect on the study site.

The Cats and Their Habits.—The mother cat, designated Cat 1, was a brindle brought to the study site in 1965. She weighed about eight lbs and was sexually altered in 1967. In 1966 she gave birth to Cat 2 (black female) and Cat 3 (gray male). Both are sexually altered, with Cat 2 weighing 12 lbs and Cat 3 weighing 16 lbs. Prior to the birth of her kittens, Cat 1 caught chiefly house mice, depositing them in the kitchen of my home. She brought rodents and young cottontails to her young, which consumed them with relish. Cats 2 and 3 began to hunt prey, and their mother's prey increased, in 1967. This expansion in predation multiplied our observations and confirmed our impression that detailed information on predation by each member of the group could be obtained. For one thing, the combined home range of the cats only encompassed selected spots within about 17 acres of fields and three acres of woods, with parts of about five adjacent acres of field habitat being used in the late fall and winter months. Secondly, the cats never ate or deposited prey where caught but instead carried it into a "delivery area," consisting of the house and lawn. The exclusive use of this delivery area was verified in 18 to 70 mammal captures per cat, as witnessed between early 1967 and late 1971.

The cats had all assumed definitive patterns of hunting and dietary habits before the study began. Cat 1 sought prey on only about five acres, which she shared with the other two; they in turn shared the balance. Cat 1 ate no prey, hunting fewer hours per day than Cats 2 and 3, each of which consumed about 90–95 percent of the microtine rodents and cottontails that they had captured. They ate varying lower percentages of their other mammalian prey.

Cat 3 was the most successful "mouser." This may have been due to its ability to leap out as much as 6 to 8 feet over 3-foot-high grass, enabling it to reach microtine rodents concealed in runways beneath dense cover. These attacks appeared guided mainly if not entirely by auditory and olfactory cues.

Prior to 1968 and throughout the study a daily allotment per cat of 150–220 g of raw beef, chicken parts, and commercial pet foods was available in the kitchen. An entry in the kitchen door enabled the cats to come and go freely between their hunting grounds and the house. All the cats slept in the house and consumed varying amounts of the food provided for them.

Recording Observed Deliveries of Prey.—Almost all of the outdoor portion of the delivery area and about six acres of the cats' hunting grounds were visible from inside the house; vantage points outside yielded a still wider view of the hunting grounds. Exploiting these advantages, the delivery of prey was monitored from a half hour to 24 hours per day on 1,387 days, during a total of about 8,500 daylight and 7,300 crepuscular-nocturnal hours. Additionally, 17 periods of three to 14 days, involving every season in nearly all the study years, were devoted to continuous monitoring of prey deliveries.

Prey items were usually weighed indoors on a fine balance scale, although a small spring scale, carried outside, was sometimes used. Most sexing was done by external features; the counting of fetuses was done by opening obviously pregnant females before allowing the cats to eat them. The only prey the cats were not allowed to eat were small series of voles appropriated and frozen for future sexing and/or identification.

The delivery area, which was rarely left unattended for longer than 48 consecutive hours, was examined and cleared of prey remains at dawn and dusk when circumstances permitted. This facilitated attribution to diurnal or non-diurnal predation of some whole and many remnant specimens stemming from unobserved deliveries. Specimens not accountable with respect to time of delivery were distributed each month between diurnal, crepuscular, and nocturnal columns, in proportion to the total specimens stemming from observed deliveries of the species. Unobserved deliveries of the day-shunning white-footed and jumping mice were allocated half to crepuscular and half to nocturnal predation, in accordance with the cats' observed pattern of catching these species.

The cats sometimes left the entrails in consuming microtines (bog lemmings, prairie and pine voles) and these remains were difficult to identify as to species. Entrails stemming from unobserved deliveries were allocated to species in ratio to the representation of each microtine in the total monthly captures recorded through observed deliveries.

Besides specimens completely devoured during the absence of observers, gaps in my records and possible misleading information may have resulted from: (a) small prey being swallowed very swiftly and not detected by observers; (b) the scavenging of prey remains by opossums, dogs and other animals, especially at night; and (c) failure to find small prey or remnants concealed under leaves and grass in the delivery area.

RESULTS

Species and Average Annual Totals of Captured Prey.—Mammals taken by the three cats in the four years of study are listed in Table 3, along with the number of fetuses killed, the average weight of the prey specimens, and

TABLE 3
AVERAGE ANNUAL PREDATION (COMBINED) ON VERTEBRATES BY THREE CATS IN UNION COUNTY, SOUTHERN ILLINOIS, 1968-1971

| Prey | Number captured ¹ | Fetuses killed | Average weight of prey ² | Combined weight of prey ² | Percent of catch |
|----------------------|------------------------------|----------------|-------------------------------------|--------------------------------------|------------------|
| Long-nosed shrew | 6.0 | 2.7 | 3 | 18 | 1.3 |
| Eastern chipmunk | 19.5 | — | 60 | 1150 | 4.0 |
| White-footed mouse | 53.0 | 32.0 | 18 | 954 | 11.0 |
| Southern bog lemming | 26.5 | — | 25 | 662 | 5.5 |
| Prairie vole | 202.5 | 225.7 | 26 | 5265 | 41.9 |
| Pine vole | 72.5 | 26.0 | 23 | 1667 | 15.0 |
| House mouse | 19.5 | — | 12 | 234 | 4.0 |
| Meadow jumping mouse | 2.5 | — | 11 | 27 | 0.5 |
| Eastern cottontail | 46.5 | — | 165 | 7672 | 9.6 |
| Other vertebrates | 35.0 | — | 38 | 1354 | 7.2 |
| Totals | 483.5 | 286.4 | 39 | 19003 | 100.0 |

¹ These figures are double the number of observed captured specimens; see text for explanation.

² Figures are to nearest gram.

related data. The figures for total prey are double the logged prey, divided by four. This assumes the study registered 50 percent of the cats' captures—a percentage roughly corresponding to: 1, the average amount of total time the the delivery area was under observation for recording prey; and 2, the number of prey items logged in the same year when the delivery area was under continuous day-and-night scrutiny, compared to the number logged (during equivalent seasonal and hourly periods) when continuously scrutinized for lesser amounts of time. Figures are not available on the rate at which scavengers expunged evidence of unobserved deliveries. If the rate was greater than I believe, the totals for captured prey given in Table 3 are low.

Diurnal predation yielded 49.8 percent of the prey items, crepuscular predation 20.1, and nocturnal predation 30.1 percent. Young cottontails constituted the leading prey by volume (40 percent). Prairie voles were the prey most frequently captured, composing more than 41 percent of all captured vertebrates and 45 percent of the captured mammals. A total of 33.8 percent of the captured prairie voles, plus 18.1 percent of the pine voles, contained fetuses (Table 4), resulting in the average annual removal of over 251 microtine fetuses.

Potential mammalian prey not known to have been caught included all age groups of opossum, mole, short-tailed and least shrews, muskrat, woodchuck, gray, fox and flying squirrels, and native carnivores. In addition, no adults of chipmunks or cottontails were taken, nor fetus-bearing bog lemmings, house mice, and jumping mice.

TABLE 4

SEX RATIOS AND FETUSES IN PREY OF THREE CATS IN UNION COUNTY, SOUTHERN ILLINOIS, 1968-1971

| Prey | Percentage of dissected specimens | | | Average number of fetuses |
|-------------------------------|-----------------------------------|--------|---------------------|---------------------------|
| | Male | Female | Gravid ¹ | |
| Long-nosed shrew (N = 10) | 40 | 60 | 20 | 5.5 |
| Eastern chipmunk (N = 36) | 44.5 | 55.5 | 0 | 0 |
| White-footed mouse (N = 34) | 52.9 | 47.1 | 11.1 | 5.5 |
| Southern bog lemming (N = 23) | 52.2 | 47.8 | 0 | 0 |
| Prairie vole (N = 152) | 52.6 | 47.4 | 33.8 | 3.3 |
| Pine vole (N = 33) | 54.5 | 45.5 | 18.1 | 2.0 |
| House mouse (N = 13) | 66.6 | 33.3 | 0 | 0 |
| Meadow jumping mouse (N = 12) | 50.0 | 50.0 | 0 | 0 |

¹ Figures signify percentage of species sample, not percentage of females.

TABLE 5
SEASONAL PERCENTAGE OF PREY CAPTURED IN BROAD DAYLIGHT BY THREE CATS IN
UNION COUNTY, SOUTHERN ILLINOIS, IN 1968-1971

| Prey | Dec.-Feb. | Mar.-May | June-Aug. | Sept.-Nov. | Total |
|----------------------|-----------|----------|-----------|------------|-------|
| Long-nosed shrew | 0 | 1.7 | 1.2 | 0 | 2.9 |
| Eastern chipmunk | 0 | 6.8 | 0.2 | 2.5 | 9.5 |
| Southern bog lemming | 2.3 | 2.5 | 0.2 | 0.7 | 5.7 |
| Prairie vole | 4.4 | 18.7 | 16.2 | 8.1 | 47.4 |
| Pine vole | 0.5 | 7.1 | 1.2 | 0 | 8.8 |
| House mouse | 0.2 | 0.2 | 0.2 | 0 | 0.6 |
| Cottontail | 0 | 4.5 | 6.6 | 0.2 | 11.3 |
| Other vertebrates | 0 | 5.1 | 7.3 | 1.4 | 13.8 |
| | 7.4 | 46.6 | 33.1 | 12.9 | 100.0 |

Comparative Seasonal Success of Diurnal Predation.—Table 5 shows seasonal differences in the frequency with which the cats obtained prey during the non-twilight diurnal hours, which is when most hunting by most hawks occurs. Almost 80 percent of these captures resulted from spring and summer predation, compared to only 7.4 percent for winter predation.

Other Seasonal Patterns of Predation.—In winter the cats sought prey chiefly during the six middle hours of the day, hunting longer on clear bright days than on overcast days, and hunting little at night and on days with both very low temperatures (below 15° F) and dark skies. In spring they hunted without seeming to concentrate on a particular period, although hunting less in mid-day and more often in twilight than before, going abroad infrequently in the middle of the night. In summer and fall they avoided mid-day to hunt mainly in the twilight periods and at night. Freezing weather inconvenienced them, yet they caught prey during and after snow storms and ice glazes; furthermore they rarely missed an opportunity to hunt prey during light rains and immediately after heavy rains.

Records from 24-hour periods of surveillance of the delivery area afford the one consistent means of gauging the average number of combined hours per day the cats devoted to hunting prey. The per day figures were as follows: approximately 14-18 hours in spring; 13-17 hours in summer; 10-15 hours in fall; and 8-12 hours in winter (Cat 1 hunted little in this season).

There were only thirteen 24-hour periods (each in April, May, and June) during which any cat was known to have caught as many as three or more specimens. The greatest number of prey items known to have been caught in a 24-hour period by the combined cats was six, and only three such instances

occurred. The average number of no-capture days per year was 174, of which over 43 percent occurred in the three winter months.

DISCUSSION

The reader who has digested my findings can imagine that a hawk visiting my study site in the winters of 1968–1971 was more apt to see a cat than a rodent. I think this a prudent speculation, and one that I wish to examine in the context of the local concentration of Red-tails, Marsh Hawks, and kestrels in late fall and winter. Although tending to include fewer participants each year (Graber and Golden, 1960; Graber and Graber, 1963), this buildup occurs annually in southern Illinois.

Potentially satisfactory hunting conditions precede the buildup as prey is probably ample and relatively active (and vulnerable) in the mild climate. Annual snowfall averages only about 11 in, as against 22 to 29 in in the central and northern portions of the state (Rodesiler and Qutub, 1973). Absent is the deep and prolonged snow cover that to the north often protects microtine rodents, the prey of greatest importance to these wintering raptors throughout the middlewestern prairie and Great Lakes regions. For example, Craighead and Craighead (1956) found meadow voles (*Microtus pennsylvanicus*) composed 84 to 98 percent of the winter diet of Red-tailed and Marsh Hawks in Michigan, and over 50 percent of that of kestrels. My observations, while limited and scattered over eight years, suggest that in southern Illinois the primary prey are prairie and pine voles, which predominated in the stomach contents of the only wintering, locally killed Red-tailed Hawks (3 specimens), Marsh Hawks (2), and American Kestrels (2) that I have been able to examine.

Birds of these species, under observation from a distance, often obtain what appear to be voles within the general area containing the hunting grounds of my cats. However, I believe that within the cats' home range only few microtines occurred during the winters of my study.

The cats themselves could find little prey of any species from December through February. We logged no specimens on 302 of 361 total winter days. I consider this striking evidence of scarcity of prey, particularly of microtines, which cats detect and seize with special facility. "I have watched cats hunting *Microtus*," Pearson (1960) commented. "The consistent success of their vigils beside runways makes *Microtus*-hunting seem absurdly easy." Other authors bear this out: for example, Bradt (1949) owned a farm cat that killed approximately 1,200 meadow voles of 1,628 mammals caught in 18 months. A cat belonging to Toner (1956) "usually brought in two or three voles each day." Especially my Cat 3, but also Cat 2, almost surely would have caught more microtines in winter if they had been able. They

both relished microtines as food and showed no inclination to omit them from their winter diet. On the contrary, they ate every vole they are known to have captured in winter. As a demonstration of their commitment to winter predation, they increased their home range by about 25 percent. Furthermore, all three cats had the advantage of combing familiar terrain on which they had monitored the microtine populations continuously throughout their hunting years: probably each was well-acquainted with the seasonal activity of these prey, at least by the winter of 1969-70.

As shown in Table 5, the hunting success of my cats rose each spring (peaking in May and June), declined steeply in fall, and became almost nugatory in the winter months. This cycle almost certainly reflected seasonal differences in density of the prey, especially of microtines. The problem is to know to what extent the cats, by their predation in spring and summer, controlled microtine reproductive cycles the year round, helping cause the depressed winter densities. Annually, from March through November, the cats removed from each acre of their combined home range (25 acres) an average of over 27 mammals-and-fetuses, of which 22.2 per acre were microtines. At the same time, no fewer than 10 species of warm-blooded native predators, along with other kinds of "environmental resistance" (i.e., litters drowned in downpours, specimens killed in mowing operations), presumably reduced the microtine populations still further. With the arrival of late autumn, non-resident hawks may well have been faced by what amounted, by then, to a near-completed harvest of microtines.

Winter Availability of Non-microtine Mammals on the Cats' Hunting Grounds.—A high proportion of the cats' winter hunting was diurnal—thus closely paralleling the diurnal pattern of hawks. It seems possible that hawks seeking mammalian prey in the same place and time as the cats would have enjoyed better hunting had the raptors taken prey that the cats either shunned (moles and shrews), could not catch (squirrels, adult cottontails), or feared to attack (adult native carnivores). Even if this occurred, it is difficult to discover an ample food supply in this list. The squirrels and cottontails consisted of few and wary individuals that had eluded one or more seasons of harvesting by sportsmen and native predators, and that, in the case of the cottontails born on the study site, had escaped the cats, which ate much of the annual crops of young. Few if any vulnerable young carnivores existed on the study site, and normally the woodchucks and chipmunks were in hibernation. The remaining potential prey included mainly moles, shrews, the few white-footed mice active on dark days and in twilight periods, and house mice: the last tended to overwinter in and around buildings, where they were more available to the cats than to hawks. As moles spend little time foraging above ground at any time, especially in winter (Hoffmeister

and Mohr, 1957), the supply of sizeable prey for hawks would appear to have been contracted seriously in the absence or unavailability of microtine rodents. I doubt that shrews, weighing only 2.7 g to 11.6 g on the study site, could have represented more than an augmentation in the diet of Red-tails, although perhaps important to Marsh Hawks and kestrels in the absence of other prey.

The Prairie Vole As Primary Prey of Hawks and Cats.—Prairie voles, I believe, would thus typically be the basic mammalian food for wintering buteos, harriers and kestrels throughout most of southern Illinois. This species frequents grassy habitats of many types (Hoffmeister and Mohr, op. cit.), haunts surface runways in daylight (except perhaps in the coldest weather), and has a tendency to develop strong populations due to a high reproductive rate (Krebs et al, 1969). Bog lemmings and pine voles are more specialized and more limited in distribution, as well as "sporadic in occurrence and usually uncommon" (Hoffmeister and Mohr, op. cit.). Accordingly, the impact of annual cat predation on the availability of prairie voles could well pose the principal threat to the success of wintering hawks in my area of study. Fetus-bearing specimens (Table 4) constituted over one-third of the prairie voles taken by my cats, and this figure excludes fertilized females in which pregnancy was undetected by the methods that I employed.

After investigating the intensity and bioenergetics of carnivore (mainly cat) predation on the California vole (*Microtus californicus*), Pearson (1964, 1966, 1971) argued that population cycles of microtine rodents may be controlled by carnivores. "The data support the theory that carnivore predation during a crash and especially during the early stages of the subsequent population low determines to a large extent the amplitude and timing of the microtine cycle of abundance." In other words, if a powerful force of carnivores remains active in the habitats of a depleted and vulnerable species of preferred prey, the carnivores may check and overpower the breeding of the prey. Cats that are fed by man, as were mine, will inevitably remain a significant force on their hunting grounds the year round, in contrast to native predators, which tend to increase and decrease in an area according to the availability of prey. If prey animals grow scarce or difficult to catch, cats with a guaranteed food supply are merely inconvenienced, whereas native predators either must leave for "greener pastures" (i.e., hawks) or face unpromising prospects and even starvation (Thompson, 1935; Pearson, 1966; Pitelka, 1961).

Krebs et al. (1969) conducted a two-year study of the cyclic demography of the prairie vole in southern Indiana. They determined maximum density to be 35–40 specimens (not including fetuses and nest litters) per acre, under more-or-less natural conditions in a favorable habitat, but usually density was

much lower, ranging from about two to 15 individuals (of "trappable" size) per acre. The Indiana study also found the prairie vole to be relatively trappable and thus easily trapped out. Given such vulnerability, spring and summer reproduction of prairie voles might be curtailed and its amplitude reduced by cats, as by trapping. This would reduce local population levels severely enough that reproduction in the non-winter months would not provide a winter abundance of specimens.

Work now in progress at my study site is investigating these and related problems, which are fraught with the complexities of environmental relationships that regulate the density of species in a given habitat at a given time (see Holling, 1959, 1965). Meanwhile, I think it is worth emphasizing that the distribution and number of cats in rural habitats are regulated less by the carrying capacity of the land and environmental resistance than by the customs and needs of the human population. No one knows how many cats are hunting prey in any part of the American country side. I recently received information from 45 of 49 queried wildlife protective agencies on the continental distribution and density of cats in the U. S.; most expressed a desire to be helpful but none furnished data established by a cat census.

PROJECTIONS

On the assumption that one-third of the estimated 31 million U. S. cats occurs in rural areas, our countryside contains 10,333,333 cats. Assuming each such cat catches prey at the same average annual rate and exploits the same average number of acres per animal as the average of my cats, then cats are removing about 5.5 billion rodents and fetuses and about 2.5 billion other vertebrates per year from a total of about 26,000 mi.² These are conservative projections, for they do not take into account young rodents that starve to death as a result of predation on lactating mothers, or the magnitude of predation by cats that catch most of their own food and more completely live "off the land." In terms of whole prey, the food requirement of one cat is about 180 g per day, or 65,700 g per year (Howard, 1957; Bouliere, 1962). My cats together did not satisfy this level during any year, nor did they in any extended period even in the spring and summer months. Yet many "farm" cats meet most of their annual food requirements by predation, with food subsidies being given them chiefly during periods when their loss of weight and begging behavior point to prey shortages (personal observation).

SUMMARY

A continuous study of predation by three rural cats was conducted in Union County, southern Illinois, from 1 January 1968 through 31 December 1971. The results estab-

lished a basis for examining the possibility that cat predation may result in depleted winter populations of microtine rodents and other prey of Red-tailed Hawks, Marsh Hawks, and American Kestrels.

Although one of the three cats never ate prey and each cat was assured an ample supply of daily food at home, all captured prey. Their combined predation removed an annual average of 483.5 vertebrates and 286.4 mammalian fetuses from a combined home range of 22 acres of field habitat and three acres of woods. By volume, the principal prey were non-adult cottontails, by frequency of captures, prairie voles. Rodents of seven species constituted 81.9 percent of the total combined diurnal-crepuscular-nocturnal catch, and over 95 percent of the crepuscular-nocturnal catch.

The cats obtained 92.6 percent of their average annual diurnal captures between 1 March and 30 November. Their hunting success in winter was very poor, probably as a result of prey shortages that their own prior predation may have helped create. It is suggested that when captures of preferred prey by skillful, experienced cats on their natal hunting grounds sharply decline, the home range of the cats contains few such prey for rodent-seeking hawks.

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BIRD POPULATIONS IN THE HEMLOCK SERE ON THE HIGHLANDS PLATEAU, NORTH CAROLINA, 1946 TO 1972

JANE P. HOLT

Bird populations were studied in selected successional stages in the hemlock sere in western North Carolina, in relation to changes that have occurred in the vegetation over a twenty-five year period. The three study areas represent mesic shrubland, intermediate hemlock-hardwood forest, and climax virgin hemlock forest, all occurring at elevations between 3,800 and 4,100 ft. The study areas were initially mapped and censused for breeding birds in 1946 and 1947 by E. P. Odum (1950). I carried out subsequent studies on the same study plots in 1959-1960 and 1971-1972. These combined data provide the basis for this paper.

All of the study areas are located within four mi of Highlands, Macon County, North Carolina. This plateau region, averaging approximately 4,000 ft in elevation, is located at the southern end of the Blue Ridge Mountains, in southwestern North Carolina. Many plants and animals typical of areas farther north are found in this area, and the annual rainfall of more than 80 in supports a luxuriant vegetation. The ecology of the Highlands Plateau has been described by Oosting and Billings (1939) and Odum (1950).

METHODS

The three study plots were censused for breeding birds by using the spot-mapping technique (Williams, 1947; Odum, 1950). Five to six censuses were taken in the mornings on each area in the period 15-30 June 1959, three times on each from 22 May-16 June 1960, and five to seven times on each from 23 May-16 June 1971 and 23 May-7 June 1972. In each daily census the locations were recorded of all birds seen or heard (indicating sex when possible), using individual copies of Odum's original maps of the study areas. From composite maps constructed at the end of each year's study, territories were delineated and the numbers of pairs of each species on each study area were determined. When the territory of a pair of birds did not lie totally within the study area, the appropriate fraction of the territory was estimated from the composite maps and from field observations. All three study areas were visited in rotation for a combined total of three to four hr each morning. Afternoon visits were used to check for nest locations. Population density figures for 1959-1960 and for 1971-1972 were converted to pairs per 100 acres and then averaged to conform to Odum's (1950) 1946-1947 data. Where study plots consisted of less than 10 acres, the density of each species was reduced by 10 percent to compensate for the small sample size (Odum, *op. cit.*).

By 1971, some of the exact boundaries of the original 6.4 acre mesic shrubland tract had become obliterated. This necessitated a remapping of this tract. The presence of old logged hemlock stumps interspersed within the secondary growth made it possible to remain within the original logged hemlock area at all times and to include all of the

TABLE 1
BIRD SPECIES AND THEIR DENSITIES ON THE HIGHLANDS PLATEAU THE HEMLOCK SERE
(A.O.U., 1957, ORDER OF SPECIES)

| Species | Pairs per 100 acres | | | | | | | |
|---|---------------------|---------------|---------------|------------------|---------------|---------------|----------------|---------------|
| | Intermediate | | | | | | | |
| | Mesic shrubland | | | Hemlock-hardwood | | | Virgin hemlock | |
| | 1946- 1947 | 1959- 1960 | 1971- 1972 | 1946- 1947 | 1959- 1960 | 1971- 1972 | 1946- 1947 | 1959- 1960 |
| Broad-winged Hawk <i>Buteo platypterus</i> | | | | | | | 2 | |
| Ruffed Grouse <i>Bonasa umbellus</i> | | | 6 | | | | | |
| Common Flicker <i>Colaptes auratus</i> | | | 6 | 10 | 7 | 4 | | 8 |
| Pileated Woodpecker <i>Dryocopus pileatus</i> | | | | | | 1 | | 4 |
| Hairy Woodpecker <i>Dendrocopos villosus</i> | | | 6 | | | | 10 | 4 |
| Great Crested Flycatcher <i>Myiarchus crinitus</i> | | | | 4 | | | 4 | |
| Eastern Phoebe <i>Sayornis phoebe</i> | | | | | | 4 | | |
| Eastern Wood Pewee <i>Contopus virens</i> | | | | 8 | 7 | 4 | 6 | |
| Blue Jay <i>Cyanocitta cristata</i> | | | 6 | | 8 | 17 | | 8 |
| Carolina Chickadee <i>Parus carolinensis</i> | | 7 | 6 | 5 | 10 | 20 | 8 | 9 |
| Tufted Titmouse <i>Parus bicolor</i> | | | 13 | | 7 | 4 | 2 | 9 |
| White-breasted Nuthatch <i>Sitta carolinensis</i> | | | 6 | | 7 | 4 | 8 | 4 |
| Red-breasted Nuthatch <i>Sitta canadensis</i> | | | | 8 | 5 | 7 | 17 | 4 |
| Brown Creeper <i>Certhia familiaris</i> | | | | | 4 | | 8 | 8 |
| Carolina Wren <i>Thryothorus ludovicianus</i> | | | | | | 7 | | |
| Gray Catbird <i>Dumetella carolinensis</i> | 42 | 28 | 16 | 25 | 27 | 30 | 16 | |
| Brown Thrasher <i>Toxostoma rufum</i> | 14 | 7 | 3 | | 4 | 7 | | |
| American Robin <i>Turdus migratorius</i> | | 14 | 3 | 2 | 10 | 17 | | |
| Wood Thrush <i>Hylocichla mustelina</i> | | 8 | 16 | 42 | 39 | 20 | 10 | 17 |

TABLE 1 (continued)

| Species | Pairs per 100 acres | | | | | | | |
|--|---------------------|---------------|---------------|------------------|---------------|---------------|----------------|---------------|
| | Intermediate | | | | | | | |
| | Mesic shrubland | | | Hemlock-hardwood | | | Virgin hemlock | |
| | 1946- 1947 | 1959- 1960 | 1971- 1972 | 1946- 1947 | 1959- 1960 | 1971- 1972 | 1946- 1947 | 1959- 1960 |
| Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i> | | 4 | 3 | 17 | 14 | 24 | 2 | 2 |
| Indigo Bunting <i>Passerina cyanea</i> | 7 | 14 | 9 | | | | | |
| American Goldfinch <i>Spinus tristis</i> | 14 | 7 | 6 | | | | | |
| Rufous-sided Towhee <i>Pipilo erythrophthalmus</i> | 14 | 28 | 19 | | 4 | 17 | | |
| Dark-eyed Junco <i>Junco hyemalis</i> | | | 9 | 8 | 20 | 30 | | 2 |
| Chipping Sparrow <i>Spizella passerina</i> | | 7 | 3 | | | | | |
| Field Sparrow <i>Spizella pusilla</i> | 22 | 35 | 6 | | | | | |
| Song Sparrow <i>Melospiza melodia</i> | 126 | 28 | 9 | | | | | |
| Total pairs | 288 | 321 | 296 | 270 | 351 | 349 | 331 | 230 |
| Total species | 8 | 22 | 35 | 21 | 28 | 30 | 19 | 23 |

1946-1947 tract during the process of remapping. The remapped mesic shrubland tract censused in 1971-1972 covered an area of 16 acres, and this acreage figure was used in computing pairs per 100 acres for this period. Although the increase in the number of species from 1959-1960 to 1971-1972 could have been affected by the increase in size of the mesic shrubland tract, I consider the increase primarily a result of change in habitat due to further plant succession. An examination of Table 1 shows the species added in 1971-1972 to be birds typical of woodland habitats.

Unfortunately, an accurate census was not possible in the virgin hemlock forest tract in 1971-1972. Only a trail around one side of this study tract remained open by that time. All remaining trails were completely obliterated by impenetrable tangles of *Rhododendron*, and my single crossing of the tract involved a great effort and progression on hands and knees. Although an accurate census was impossible, it was possible to walk along the open trail and identify the calls of birds breeding in approximately one-fourth of the study tract. This was done on eight mornings in 1971-1972.

Although more refined statistical methods of analyzing bird species diversity exist today, the breeding bird density (in pairs per 100 acres) of one plot is compared with that of another plot according to the "percentage difference" method of Odum (1950). This allows the data from the 1959-1960 and 1971-1972 studies to be treated by the same method as the 1946-1947 data. For example, in comparing avian density in the mesic shrubland with that in the intermediate hemlock in 1959-1960 (Table 1), the species-

by-species difference in pairs per 100 acres are first calculated: e.g. for the Chestnut-sided Warbler the value is 49 and for Gray Catbird it is one (scientific names of birds are given in Table 1). All of the differences are then added, and that total difference is divided by the total number of pairs per hundred acres in the two tracts. The percentage difference is a rough index of difference (or similarity) in species composition and in density. A percentage difference at the low end of the scale indicates a close similarity, while one at the higher end shows that the populations are markedly different.

THE STUDY PLOTS

Mesic Shrubland

The example of this primary successional stage of the hemlock sere is located four mi east of Highlands, North Carolina, on U.S. Highway 64, downstream from the Virgin Hemlock Forest study area. In 1946–1947, Odum (1950) described the vegetation as consisting “. . . of shrubs and small trees chiefly alders, willows, and brambles (*Rubus*) which form dense thickets interspersed with more open areas dominated by grasses and herbs. Huge stumps of hemlock and thickets of laurel (*Kalmia*) and rhododendron remain from the original hemlock forest which occupied the area. The plot has never been cultivated, but has apparently been subjected to some grazing in the past.”

Of the three study plots, naturally the mesic shrubland has undergone the greatest change during the twenty-five years since 1947. Approximately one acre of this tract has continued under intermittent grazing or cultivation. An additional acre appears to have been disturbed by 1971–1972. The size of the tract censused in 1946–1947 and 1959–1960 was 6.4 acres. As explained earlier, the censused area was enlarged in 1971–1972 to 16 acres, including the two which had been disturbed in the past.

In the disturbed area, blackberry (*Rubus* sp.) forms a dense cover, with herbs and grasses covering the more open areas. A dense stand of sassafras (*Sassafras albidum*) has grown up at one end. The stream runs through a portion of the disturbed area. The remaining part of the study tract is covered with maples (*Acer* spp.), oaks (*Quercus* spp.), birches (*Betula* spp.), tulip poplar (*Liriodendron tulipifera*), cherry (*Prunus* sp.), sourwood (*Oxydendrum arboreum*), Fraser magnolia (*Magnolia fraseri*), locust (*Robinia* spp.), dogwood (*Cornus* spp.), and hemlock (*Tsuga* spp.). Thickets of rhododendron and laurel persist along the stream. Stumps of the old logged hemlocks may still be seen. In some cases hemlock sprouts from these stumps have produced trees more than twenty ft in height. The forest canopy averages approximately 20 ft in height, with some individual maples and hemlocks 30 to 40 ft high. The plot is in an intermediate stage of succession, but will continue to be termed the “mesic shrubland” for purposes of comparison.

Intermediate Hemlock-hardwood Forest

The example of this secondary successional stage covers an area of 15 acres, located around the Highlands Biological Station but excluding the clearings for the buildings, etc. Most of the trees are hemlock, white pine (*Pinus strobus*), birch, and maple, with evergreens comprising approximately 50 percent of the total. Most of these trees comprise second growth, but some are quite large and may represent remnants of the original virgin forest. Dense stands of rhododendron, laurel, witch hazel (*Hamamelis* sp.), and azalea (*Rhododendron* spp.) form the understory. Little change has occurred in this tract since 1946–1947, except an increase has occurred in the size of the trees and the density of the understory in some areas. The size of the tract was decreased slightly with clearing for the erection of some new buildings at the Highlands Biological Station.

Virgin Hemlock Forest

The final successional stage studied is the virgin hemlock forest, a 12 acre tract located four mi east of Highlands on U.S. Highway 64 (opposite the Mesic Shrubland). In 1946–1947, Odum (1950) stated that three-fourths of the stand was comprised of hemlock trees three to four ft in diameter and 400 or more years old. This virgin forest is a remnant of a once extensive stand of hemlock known as the "Primeval Forest" or "Ravenel's Woods." Large black birch (*Betula lenta*), red maple (*Acer rubrum*), Fraser magnolia, red oak, and other deciduous trees are widely scattered through the stand. Rhododendron makes up the dense understory.

This plot has been subjected to one man-made alteration since 1946, the addition of a small pond (approximately 30 by 50 ft), close to the center of the study area. Observations of the species nesting there in 1959–1960 indicated that the pond did not affect species or numbers of breeding birds during that period. At that time access to the interior of this forest was gained along primitive roads around part of the perimeter and paths to the center. By 1971–1972 these had become obliterated by rhododendron.

RESULTS

Table 1 shows species composition and densities of birds in the three study areas of the hemlock sere. Bird names are listed in A.O.U. Check-list order (1957; Eisenmann et al., 1973). In the interval from 1946–1947 to 1959–1960, 14 additional species were added in the mesic shrubland, eight in the intermediate hemlock-hardwood tract, and eight in the virgin forest. One species which occurred in the intermediate hemlock-hardwood forest in 1946–1947 was not found in 1959–1960 and four species were absent from the virgin forest. In the 1971–1972 census, fourteen additional species were

TABLE 2

PERCENTAGE DIFFERENCE IN THE BREEDING BIRD POPULATIONS OF THE THREE STUDY PLOTS
COMPARED WITH EACH OTHER

| | Census year | | |
|--|-------------|-----------|-----------|
| | 1946-1947 | 1959-1960 | 1971-1972 |
| Mesic shrubland and virgin hemlock | 97.9 | 83.5 | — |
| Mesic shrubland and intermediate hemlock | 95.8 | 70.2 | 50.1 |
| Virgin hemlock and intermediate hemlock | 50.5 | 33.2 | — |

recorded in the mesic shrubland and one species found in 1959-1960 was absent, while five species were added in the intermediate hemlock-hardwood tract and three species were absent. The number of species common to all three tracts increased from one in 1946-1947 to seven in 1959-1960.

Percentage differences (Table 2) showed marked declines. The decrease is particularly striking when the mesic shrubland is compared with the intermediate hemlock-hardwood forest, the value shifting from 95.8 percent in 1946-1947 to 50.1 percent in 1971-1972.

Table 3 shows the species of birds common to both mesic shrubland and intermediate hemlock-hardwood tracts increased from 12.5 percent in 1946-1947 to 65.7 percent in 1971-1972. The greatest change in bird species richness on any of the tracts during the twenty-five year period occurred in the mesic shrubland, where the number of species increased from eight in 1946-1947, 22 in 1959-1960, and 35 in 1971-1972.

Although the virgin tract was too dense for accurate census in 1971-1972, two additional species were recorded during visits to this tract. The Golden-crowned Kinglet was consistently present both years and a nesting Rufous-sided Towhee was noted in 1971.

TABLE 3

COMPARISON OF BIRD SPECIES COMPOSITION OF MESIC SHRUBLAND TRACT WITH
INTERMEDIATE HEMLOCK-HARDWOOD FOREST TRACT

| Census year | Total species mesic shrubland | Species common to both tracts | Percentage of species common to both tracts |
|-------------|----------------------------------|----------------------------------|---|
| 1946-1947 | 8 | 1 | 12.5 |
| 1959-1960 | 22 | 12 | 54.5 |
| 1971-1972 | 35 | 23 | 65.7 |

DISCUSSION

In the 1946-1947 census, only the Gray Catbird was found in all three study areas. By 1959-1960, the number of species common to all three study areas had increased to seven. Calculations of the percentage difference of the three study plots also confirm greater similarity. The difference between the mesic shrubland and intermediate hemlock-hardwood tracts decreased from 95.8 percent in 1946-1947 to 70.2 percent in 1959-1960 and 50.1 percent in 1971-1972.

The species in common between mesic shrubland and intermediate hemlock-hardwood tracts over the twenty-five year period increased from 12.5 to 65.7 percent. The similarity of species in the three plots would have been even greater in 1971-1972, if the entire mesic shrubland plot had been left undisturbed. Disturbance served to maintain prime habitat for several species characteristic of early stages of succession. These include such birds as the Song and Field Sparrows and the very high concentration of Chestnut-sided Warblers. The American Goldfinch, Indigo Bunting, Yellow-breasted Chat, Chipping Sparrow, Golden-winged Warbler, and Northern Yellow-throat also occurred in the area. These nine species, together with birds characteristic of the later successional stages, account for the high figures of 35 species and 296 pairs listed for this period.

The former mesic shrubland is now entering the intermediate hemlock-hardwood stage, as is evidenced by the presence of the Blackburnian Warbler which now breeds there. Bent (1953) describes this bird as nesting to heights of over 80 ft above ground in coniferous trees, with males singing from tall trees. The habitat preference of this bird and its presence in this study tract certainly reflect the degree of plant succession which has occurred.

The number of species represented within all seral stages in the 25 year period has increased markedly. The most dramatic increase shown in this study is in the mesic shrubland where the number increased from eight to 35 species. The increases in the intermediate hemlock-hardwood forest from 21 to 30 and in the virgin forest from 19 to 23 species (in the first thirteen years of this study) are less striking.

Kricher (1972) found that bird species richness at all seasons increased with the age of the seral stages. When the Highlands area seral stages are compared with each other, however, species richness peaked as the former mesic shrubland entered the intermediate hemlock-hardwood stage (1971-1972), rather than in the climax virgin forest. Mesic seres are known to have peaks in avian diversity in the middle rather than at the end (Adams, 1908; Aldrich, 1943).

While the number of species increased within each seral stage, the number of individuals in the virgin hemlock tract declined markedly from 331 pairs

per 100 acres in 1946–1947 to 230 in 1959–1960. This decline probably can be attributed to continued growth of the rhododendron understory, which characteristically is poor bird habitat.

Several observations concerning the distribution of particular species are of interest. Odum (1950) noted in 1946–1947 that the Highlands area lacked such northern species as Golden-crowned Kinglet, Magnolia Warbler, and Black-throated Green Warbler. Recently, Johnston (1964) lists the Golden-crowned Kinglet as an uncommon permanent resident of the area, and a nest was found in Highlands on 11 June 1951. In 1971–1972, I recorded this species consistently as a breeding bird of both the intermediate hemlock-hardwood and virgin hemlock forests. Johnston (1964) classifies the Black-throated Green Warbler as a summer visitor of the Highlands area, but with no definite evidence of breeding. I observed this species in the virgin hemlock forest tract once during the census of 1959 and again in 1960. As it was not observed more than once, it was not included in the breeding bird list; nevertheless, its presence during the breeding season may indicate that further study will prove it to be a member of this breeding avifauna. The Magnolia Warbler, although a regular migrant, has not been recorded as a summering or breeding species.

Another species which appears to have extended its breeding range into the Highlands plateau is the Brown-headed Cowbird. This bird was not recorded in the pre-1972 breeding bird counts, and Johnston (1964) classified it as uncommon—with only one observation appearing on the Highlands Biological Station records. In 1972 this cowbird appeared in both the intermediate hemlock-hardwood forest around the Highlands Biological Station and in the mesic shrubland, four mi east of Highlands. Both adults and young were commonly noted in May and June and its population density should be monitored in the future.

SUMMARY

Breeding bird population studies were carried out in the hemlock sere at elevations of 3,800 to 4,100 ft on the Highlands Plateau, western North Carolina, over a twenty-five year period. Populations of three carefully selected stages of succession in the sere (mesic shrubland, intermediate hemlock-hardwood, and virgin forest) were studied using the spot-mapping technique. Breeding bird population analyses in 1959–1960 and 1971–1972 were compared with the initial survey of these study areas by Odum (1950) in 1946–1947, and population density and species composition were compared with changes in the vegetation. Increases in density and species richness were correlated with the age of the seral stages, as evidenced by comparing percentage differences in bird populations of the study areas in the different census years. Both avian density and species richness showed an increase in the intermediate stage and a decline in the climax stage of the hemlock sere.

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EARLY BREEDING SEASON BEHAVIOR OF DOWNY WOODPECKERS

LAWRENCE KILHAM

The present report is one in a series on my studies of the year-round behavior of Downy Woodpeckers (*Dendrocopos pubescens*), done with an idea that it is only against a background of the total natural history of a species that selection pressures operative in its evolution are likely to be understood. My previous reports on *D. pubescens* have included winter and sexual differences in feeding, copulatory behavior as related to courtship, and a preliminary one on the entire breeding season that gives descriptions of the main vocalizations and displays (Kilham, 1962, 1970, 1974). Present observations, made in Lyme, New Hampshire between 1961 and 1974, supplement the 1962 report. Other accounts on the behavior of this species include those of Bent (1939), Staebler (1949), Lawrence (1967), and Short (1971), the last giving details of the displays of various species of the genus *Dendrocopos*, which in his terminology is called *Picoides*.

Although the various aspects of early breeding season behavior take place concurrently, for convenience I have divided them into: agonistic and territorial behavior as seen in winter and spring; types of drumming; courtship flights; the search for a nest site; and finally the dependence of successful courtship and nesting on an adequate environment.

AGONISTIC AND TERRITORIAL BEHAVIOR

Displacings.—The following descriptions of fall and winter interactions between the sexes are given by way of background to those seen in the early breeding season. Thus on 26 September 1968 a male displaced a female five times in 15 min, and a month later another male displaced a female four times in less than 10 min. These displacings, which continue during winter months and are often accompanied by the aggressive *chrr* note, do not always involve the seizure of a better feeding spot; often they appear as an assertion of male dominance, and this results in spacing out the sexes in relation to feeding (Kilham, 1970). Female Downies usually move away a short distance without appearing disturbed if displaced by their mate. On other occasions, I have seen female Downies react by holding strained, bill-forward poses, swinging under a limb as in combat, or opening their wings in a threat display to the male. Supplanting attacks of a somewhat similar nature are described by Short (1971) for the Nuttall's (*D. nuttallii*) and the Ladder-backed (*D. scalaris*) Woodpeckers.

The seeming hostility of male to female was reflected by the reaction of male B (MB) to his mate-to-be in mid-winter in a woodland swamp. MB nested with the same mate (FB) in 1971 and 1972 and remained on the breeding territory alone in the intervening winter. I never saw FB in the swamp at this time with exception of 29 January 1972, when she flew to within one m of MB. He swooped at her immediately, making *check*, *check* and *chrr* notes as he drove her away. This hostility was in contrast to the behavior of a nearby pair of Hairy Woodpeckers (*D. villosus*) that had started courtship in late December.

Territorial behavior.—If one accepts Noble's (1939) definition of territory as "any defended area," then four types of territorial behavior and hence territories are observable among Downy Woodpeckers. The first two, occurring mainly in fall and winter months, are exhibited by lone individuals of either sex. These types of territory are: 1, small areas with definite boundaries in some directions, in localities where feeding conditions are favorable (Kilham, 1970); 2, the area in close vicinity of a roost hole, a situation where females may drive off males as well as other females; 3, large areas claimed by a pair in the early breeding season; and 4, smaller areas around the nest hole.

The characteristics of last two types of territory are brought out in the examples of conflicts given below. Examples I and II (below) relate to early breeding season territories which, although hard to estimate, may be as large as 10 to 15 ha. Their main function, it would seem, is to provide an area where the members of a pair of Downies can search for nest stubs. Really suitable stubs are in short supply in most areas, and their scarcity appears to be an important limiting factor in breeding success, at least in New Hampshire. A fourth type of territorial behavior, appearing once a nest site is established, is defense of the area around it. This type, also noted by Lawrence (1967), is illustrated by Example III (below).

I. On 10 February 1968 male A and a rival fought on trunks of small saplings along their common border from 07:20 to 07:35. They were often within 18 cm of each other in bouts of bill-waving dances, as well as in intermittent pauses of resting in strained postures. The section of woods where the males fought was 50 m from where pair A nested the following May.

II. On 28 March 1971 in woods deep in snow, two male Downies fought in a prolonged conflict from 07:05 to 08:10, along a rough boundary line 20 m long. Features of this boundary encounter were 1, nearly all of the fighting was low down on small saplings; 2, one male might swoop down at the other, which was usually able to shift around the tree in time to avoid contact; 3, on one occasion one male seized the other, coming away with

a bill full of small feathers which stuck to his bill, as he did a bill-waving dance, and 4, a female remained in the vicinity, and the fighting became most intense when she came close to the contending males.

III. On 25 April 1965, I noticed two pairs of Downy Woodpeckers approaching each other at 06:30. The two males began fighting almost immediately. The conflict was brief, intense, and accompanied by little display. As it was fought close to a stub where one of the females had tapped briefly, it seemed probable that the two pairs of woodpeckers were contending for a potential nesting site. The owner male carried on exaggerated pecking and feeding displacement activities after his rival had left. Other accounts of the agonistic behavior of *D. pubescens* are given by Short (1971), Bent (1939), and Staebler (1949).

DRUMMING

The onset of breeding behavior is marked by drumming, as well as by territorial conflicts, that begin in mid or late winter. There is little that is stereotyped about the drumming of *D. pubescens*. It varies in rate with a bird's emotional intensity and in carrying power with the type of substrate, e.g. whether this be a hollow place, one of solid hardwood, or an indifferent one of no particular resonance. Both sexes drum, but females often do more drumming than males. The total amount of drumming varies with circumstances; a pair that has found a nest site early in the season drums relatively little, while a pair located in woods deficient in suitable stubs drums a great deal. Among types of drumming that are distinguishable in relation to circumstances are the following:

Mate-location.—This usually consists of only a few bursts, needed when the birds of a pair are feeding separately over a wide area, as they often are.

Dawn-rendezvous.—The efforts of a Downy Woodpecker to locate its mate at the start of a day can be prolonged, especially where roost holes are far apart. A female, for example, began drumming at 05:11 on 14 April at a rate of 18 bursts per min. Her mate came from his roost hole 3 min later and flew in her direction. He stopped on a dead pine to drum before reaching her, and she, after more drumming, then came closer to him.

Contact or contentment.—When Downy Woodpeckers are under no pressure to find a nest stub, either because it is early in the season or because they have already found one, one or the other of the pair, but particularly the female, may rest in the sun or some high dead limb, preening in a prolonged leisurely fashion and drumming in pauses in between. Such activities may, it would seem, promote the pair bond in relation to a particular locality.

Duetting.—Lawrence (1967) writes of reciprocal or answering drumming as occurring in March, at the onset of the breeding season. There are, how-

ever, two kinds of answering drumming. The first of these promotes the pair bond: when the affairs of a pair are going well, each bird drums, on occasions in unhurried fashion in response to the drumming of the other, with resting or preening in between.

The second type of duet drumming I refer to as a tug-of-war type. When relations between the members of a pair are disturbed, the male having preference for one nest stub and the female for another, each drums in an effort to entice the other to come and inspect the chosen site. Drumming can then be prolonged and the rate expressive of the intensity of the disagreement.

Displacement.—Downies, like Hairies and a number of other woodpeckers, drum as a displacement activity at the presence of an intruder, whether this be a conspecific or otherwise. The drumming is usually done where the woodpecker happens to be. On 11 April 1969, for example, a foreign female arrived in a territory, and was attacked by the female of the owner pair. The male did not participate in the conflict but immediately started to drum at a fast rate of 12–20 times a min.

Whisper.—When a nest excavation is on its way to completion, the members of pairs may respond to each other with low drumming; this appears to be expressive of a close pair bond. On 23 April a female, drumming close to a hole subsequently used for nesting, was answered in similar fashion by her mate in the woods nearby. Six days later I saw the reverse situation, with the male drumming by the nest cavity. Drumming softly, however, is not always a matter of a duet. A female near a completed nest cavity may occasionally drum in this manner wherever she happens to be.

Copulatory.—Downies of either sex, but chiefly the male, may drum when ready for copulation, thus attracting its mate from a distance. This is one of a number of types of drumming also noted for *D. villosus* (Kilham, 1966).

Territorial.—Drumming from a high place may have a function in proclaiming territory. Drumming of this type can, as a side effect, attract rivals and precipitate conflicts, thus possibly, hastening, settlements of territorial disputes before the time of actual nesting.

Downies, like other species of woodpeckers, have drum trees (such as the hard wood at the top of a dead maple) that have special resonance. A male Downy may ascend such a place, trying successive spots with a few bursts on each, extracting a variety of sounds, some flat, some deep, and others loud and sharp, the effect being like the playing of a xylophone. It should be emphasized that some types of drumming, as for example in conflicts or of the whisper type, may be done on places of indifferent resonance wherever the Downy happens to be.

Some pairs of Downies, and particularly those that have no potential or

actual nest site on which to center activities, resort to one particular drum tree as a rendezvous, as though a center of some sort were needed for the pair bond. Lawrence (1967) cites the example of one male that came to such a tree for three years. I have noted three such headquarter trees. On one of these the female, arriving in response to the male's drumming, started drumming three m below him in an irregular duet. From this and comparable experiences with other pairs, it would seem that males can attract females to headquarter trees.

SEARCH FOR A NEST SITE

Downies, as in woodpeckers such as the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Kilham, 1971), appear to have a search image of an optimal nest site. This image appears, in New Hampshire, to be the broken off, dead top of a living tree. Both sexes search for nest sites as is brought out below:

I. On 24 April a female moved slowly over the broken top of an old butter-nut (*Juglans cinerea*), giving an occasional burst of drumming and percussing here and there. After 5 min she tapped briefly near the top of the tree as her mate flew to her. She left as he arrived. He then inspected the stub and left.

II. On 20 April a male Downy drummed on the top of an aspen stub for 3 min, then took a bill-forward pose on seeing his mate. He then moved to the rear of the stub, tapped a few times, and flew off in a ruffle flight (Kilham, 1962) as she arrived.

The above examples illustrate a spectrum of behavior that I have observed at over 30 potential nest sites. Either the male or the female locates a potential nesting stub and then drums for its mate. As the mate approaches, the bird on the stub taps briefly and leaves. The drumming and the tapping are not always in pure form, for sometimes they are intermixed. The arriving bird inspects the stub superficially or more thoroughly percussing as it goes. It may take a number of such inspecting visits before a stub is accepted or rejected. The longer the second Downy spends on the stub, especially if it remains on it to preen in a leisurely fashion, the more likely that it is interested in it as a nest site. Whether the female or the male is taking the lead is difficult to say because an observer never knows for certain that he has seen the whole sequence of events.

COURTSHIP FLIGHTS

These fluttering or gliding displays are alike and are used in the same ways in *D. pubescens* and *D. villosus* (Kilham, 1962, 1966). Table 1 summarizes 33 flights observed for *D. pubescens* in the breeding season. The majority were by males and appeared to strengthen attachment to an actual

TABLE 1
SUMMARY OF 33 COURTSHIP FLIGHTS OF DOWNY WOODPECKERS WITH CONTEXTS
IN WHICH THEY TOOK PLACE

| Phase of breeding and dates of observations (inclusive) | Partner displaying | Direction of flights | Number of observations |
|---|--------------------|--|------------------------|
| Drumming; search for nest site (15 Feb.-2 Apr.) | F | To tree where M feeding | 1 |
| | M | To tree where F feeding (no displacing) | 1 |
| | M | From a potential nest stub | 2 |
| | F | To M by a potential nest stub | 1 |
| | M | From drum place as F came to it | 1 |
| Triangle conflicts (17 Feb.-16 Apr.) | M | To vicinity F-F conflict | 2 |
| | F | To vicinity M-M conflict | 1 |
| | F | F-F conflict, M nearby | 5 |
| Excavation of nest; copulation (27 Apr.-24 May) | M | To hole, F probably nearby | 9 |
| | M | To F; pre-copulatory | 7 |
| | M | From hole as F came to it | 1 |
| Incubation (11 May) | M | To F; pre-copulatory | 1 |
| Late nestling (14 June) | M | M & F by hole. M flew off | 1 |

or potential nest site. As described elsewhere (Kilham, 1974), Downies copulate close to excavations. Many of the courtship flights, from the nest hole to the branches where copulations took place, were to the female and were precopulatory in nature. They ceased, with one exception, at the time of incubation. Downies may experience a recrudescence of breeding behavior at the end of the nestling period and this may explain the courtship flight then. The courtship flights of females, when two of them were fighting for a single male, stimulated a high pitch of emotion. The fact that I never saw these displays in territorial conflicts of a male against a male or a female against a female, made it seem likely that the displays, in the triangular contests, were sexual in nature.

DEPENDENCE OF SUCCESSFUL COURTSHIP
ON AN ADEQUATE ENVIRONMENT

Successful breeding depends on a habitat that offers what is needed. Nothing is more striking than the differences between the way in which a pair of Downies that has found a good nest site goes about nesting and the behavior of a pair that tries one potential nest site after another, finding all inadequate. Good nest stubs are nearly always in short supply. When an adequate site is lacking, the pair bond breaks down and the male begins

a period of prolonged drummings, seemingly in an effort to get his mate to return. These contrasting situations, one representing breeding success and the other failure, are brought out in the histories of pairs A and B below. The behavior of pair A was noteworthy in presenting in almost classic fashion the main forms of courtship observable in *D. pubescens*.

History of pair A.—The territory of pair A appeared favorable for nesting in a number of aspects. One was that it included paper birches that furnished a winter food supply (Kilham, 1970), and this permitted the members of the pair to stay more or less together in winter months. Signs of a pair bond were evident as early as 11 January 1968, when I saw the two birds feeding only 15 cm apart. When the male flew, the female followed. A week later the female persisted in staying in the vicinity of the male, in spite of his supplanting attacks; on 4 February he flew to her in floating, courtship flight. Seemingly uncertain of his intentions this early in the season, she faced him with bill pointed straight forward, as if to meet an attack. As the winter and spring of 1968 were unusually cold, this early onset of breeding behavior was certainly not attributable to mild weather.

On 17 February the Downies were together from 06:50 to 07:15. Male A (MA) drummed briefly and his mate, moving up a potential nest stub, gave a series of loud, single taps, and drum-taps near the top.

On 11 March when MA alighted on the dead top of a live red maple (*Acer rubrum*) that was to become the nest stub in May, he was displaced by FA in a reversal of the usual dominance. FA then rested, preening in leisurely fashion. That the stub was regarded as a nest site, although no excavating had been done, was evident on 30 March when the two Downies attacked a female Hairy Woodpecker that came close. In these attacks the female Downy was more persistent and aggressive than the male.

A variety of other behavior at this time indicated closeness of courtship. On both 30 and 31 March, for example, MA flew across the open swamp from the nest stub with wings held in a V, as he tilted from side to side in courtship flight, and later FA preened in leisurely fashion close to the stub while MA rested motionless. On 6 April MA and FA had a drumming duet, one answering the other in unhurried fashion.

I witnessed copulations of pair A by their maple stub on 2 May, and by 8 June the young were ready to leave the nest. This pair thus had had an exceptionally early start on their nesting and were able to fledge the young about 2 weeks ahead of most pairs that I have watched in New Hampshire. This earlier breeding of resident as compared to a migratory pair of Downies is also described by Lawrence (1967).

Breakdown of breeding behavior.—In 1968 two pairs (including B) of Downy Woodpeckers nested successfully in a wood of 15 or more ha. In the

following year, I sought to follow the breeding behavior of these two from its earliest onset through to the time the young were fledged. Neither pair proved able to establish a nest. From following the birds through April into May it was apparent that they had inspected every possible site; in the young woods growing up after lumbering some years before, however, there were no dead stubs of the right type remaining.

The members of the pair B exhibited the usual signs of courtship and a developing pair bond in April 1969. In absence of any nest site or potential one, the male often drummed and preened on a slanting maple, his head-quarter tree: it was there that he met his mate at dawn. There was a dead stub nearby, obviously inadequate for nesting, but on 14 May MB and FB both flew to it in courtship flight. This was the last I saw of the two together. The behavior of MB showed a change on the following day. He was resting on the slanting maple in the early morning with feathers fluffed out, head drawn in, while looking about restlessly. His mate did not appear then, or on the following day, when he began the prolonged drumming that was to last well into June.

DISCUSSION

Points from the foregoing reports needing comment are the nature of the bill-waving dances, of the courtship flights, and of the dominance relations between members of pairs.

Bill-waving dances.—The dances of both *D. villosus* and *D. pubescens*, when performed in persistent fashion, have always, in my experience (Kilham, 1959, 1962, 1966, 1969), been used in territorial conflicts of male against male and female against female. Bill-waving can be used against non-specific intruders, such as Starlings (*Sturnus vulgaris*), by a nest hole, but then only briefly. It is confusing, therefore, that some authors have regarded the dances as courtship. F. H. Allen in Bent (1939) gives good descriptions of the dances of both *villosus* and *pubescens*, yet refers to the woodpeckers as courting when admitting that he was unable to identify the sexes. Identification of the sexes is indeed not always easy. The head-back position involved in the dances compresses the males' red nuchal patches, making them less visible; this is a situation one would hardly expect if the dances were sexual in nature. Staebler (1949) also misconstrues the nature of the dances by referring to bill-waving between two males in the fall as being courtship. This is a use of the term that lies outside of all usual definitions (Thomson, 1964). A male Downy may attack an intruding female Downy, and vice versa. In such situations, which are usually by nest (Kilham, 1974) or roost hole, the attacks are direct with little display.

A question is why two male Downies should face each other, in a small stretch of woods in March, in bouts of bill-waving that may go on for over an hour. Several answers are conceivable. One is that the boundary being new, neither male has a psychological advantage over the other. Under these circumstances each might fight equally hard in any direct conflict, and this could lead to injury. By holding their weapons, i.e. their bills, upward and back in a position ineffective for striking blows, the rivals are able to face each other in a ritualized conflict that is relatively harmless. A second point is that the prolonged nature of these conflicts may have value in imprinting: that is in forcing each male to become very well-acquainted with that small bit of woods where the prolonged conflict occurred.

Courtship flights.—I have interpreted the aerial displays of *D. pubescens* as courtship, and this appears to be that also of Lawrence (1967), whose few descriptions (op. cit.:59, 77) fit in with the observations given in Table 1. Pynnönen (1939) describes similar flights in the Greater (*D. major*) and Lesser (*D. minor*) Spotted Woodpeckers. He also links these with courtship, regarding them as expressive of high excitement. Short (1971), on the other hand, takes an opposite point of view and regards "flutter aerial displays" as being clearly agonistic. His observations are different from mine as regards contexts, and I am not sure whether we are following the same criteria or observing the same phenomena.

In relation to possible agonistic components to courtship flights there are three points that should be made, one being that occasionally a Hairy (Kilham, 1966) or a Downy Woodpecker (and usually a male) may hold its wings out in a position of full threat display when about to alight close to a rival. These short displays seem to me to be purely agonistic and unrelated to the more prolonged fluttering or gliding flights used in courtship. A second point is that courtship flights can occur in the context of two females or two males fighting in the presence of the mate of one of them. Sexual emotion can be intense at these times, as shown by the copulations that may take place with both Hairy (Kilham, 1969) and Pileated (*Dryocopus pileatus*) (Kilham, 1959) Woodpeckers under the same circumstances. It is as if the emotion built up by agonistic were directly transferable to sexual behavior.

A third point is that in some cases courtship displays appear to have been derived from what were originally threat or agonistic displays. By this derivation, displays that relate entirely to courtship in one species may still have a hostile connotation in some related species. An excellent review of this subject is given by Andrew (1961). Although he deals with passerines, much of what he reviews may apply to some picine displays as well. I am not sure that the courtship flights of *D. pubescens* or *D. villosus* have any such derivation. They would seem, on the contrary, simply to be a normal

activity (i.e. flying), carried out in an exaggerated manner, a phenomena discussed by Lorenz (1970) for geese and, amusingly, for man.

Sexual dominance.—That female Downy as well as Hairy Woodpeckers occasionally take the lead in breeding behavior is a subject worth more attention than it has received. Lawrence (1967) recognizes the problem and states that the male of *D. villosus* is dominant in nesting, while a reversal of roles in favor of the female exists in *D. pubescens*. Drawing upon other experience, it appears to me that females of both species occasionally take the lead, either temporarily or for longer periods, although this is not the usual situation. In Maryland, for example, I encountered a female of *D. villosus* (Kilham, 1960) that did an extraordinary amount of drumming in winter months in attracting a male to her territory; I also encountered a somewhat similar situation, of milder degree, in New Hampshire (Kilham, 1969). Among Downies, males do by far the larger part of the excavation of nest holes as described both by Lawrence (1967) and Kilham (1974). Yet in an earlier set of observations (Kilham, 1962), I encountered several females that did the larger share. This reversed situation was also noted by Shelly who, as quoted in Bent (1939), wrote that of "a number of nests observed I have never known the male Downy to assist in excavating."

A possible explanation of these departures is that the dominance relations between members of pairs of Downy Woodpeckers represent something of a "see-saw." As long as males continue to exert dominance, females remain subordinate. Various factors may lead to a temporary or longer-lasting reversal of dominance. These are matters needing further study. From observations on woodpeckers of a number of species, including some that were hand-raised and kept in an aviary (Kilham, ms), it seems that females have a drive to assume male behavior, but are kept from doing so by the dominance of their mates. This situation is described by Lorenz (1970) in his classic paper on "The role of the companion in the bird's world." In terms of survival value, increased female dominance in Downies means that, whenever the male does less of an activity such as excavating, his mate will fill in and do more.

Temporary reversals of dominance may be encountered in most pairs of Downy Woodpeckers. One instance noted in March in the present study was where the female of pair A drove her mate from what was to become the nest site in May. No two pairs of this species, however, will ever be found to behave exactly alike. Individuality, prior experience in nesting, and environmental factors can all lead to a diversification of behavior, particularly in the early breeding season.

A final point is the seeming hostility that exists between members of pairs of *D. pubescens* early in the breeding season. This hostility may relate to

feeding habits. Downies generally appear to have a difficult time finding prey in winter months, judging by the hours spent foraging (Kilham, 1970). Intrapair hostility, stemming largely from the male, may serve to separate members of a feeding pair in the early spring as well as winter. This situation prevents the formation of a close pair bond in March and early April. What brings the members of a pair to the close association needed for nesting is the possession of an adequate nest site that will serve as a center for courtship activities and, eventually for copulations, which almost always take place in its vicinity (Kilham, 1974).

SUMMARY

Male and female Downy Woodpeckers remain separate during winter months, when supplanting attacks by the male keep the two spaced out in relation to feeding. Early breeding behavior usually begins in March in New Hampshire and is marked by prolonged territorial conflicts, accompanied by bill-waving dances between males. Drumming, of which a number of types are described, serves to bring the two sexes together as well as having a territorial function. Signs of an increasing bond between members of pairs are that the two travel together at times in foraging, the female tolerating supplanting attacks by the male, and that when the male flies the female follows. Either member of a pair may percuss a stub to determine its suitability for the excavation of a nest, then drum or tap to attract its mate.

Once a nest stub is found, signs of increasing harmony between the members of pairs are leisurely preening, one of the pair resting motionless in the presence of the other, duets of drumming, courtship flights, and joint defense of the nest stub against potential competitors. When no adequate nest site can be found, the pair bond breaks down, the female leaving while the male remains in the territory, carrying on prolonged drumming over many weeks. Dominance by the male partner, occasional reversals of dominance where the female takes the lead, the nature of the bill waving dance, and courtship flights are discussed.

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BREEDING AND ANNUAL CYCLE OF LAUGHING GULLS IN TAMPA BAY, FLORIDA

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The Laughing Gull (*Larus atricilla*) is one of the most familiar species of the coasts of the eastern United States. Although the behavior of this gull has been intensively studied (e.g. Beer, 1970a, 1970b; Impeken, 1973), many aspects of the breeding biology are little or poorly known. Our study was designed to gather data on reproduction in this species in Tampa Bay, as well as to provide an outline of the annual cycle in that area. A better understanding of the biology of this species is particularly relevant, in view of man's general encroachment into its breeding areas and of the alarming decline in populations in New England (Nisbet, 1971).

STUDY AREA AND METHODS

Laughing Gulls have been recorded nesting in the Tampa Bay region since the early 1900's (Sprunt, 1954). In recent years they have nested primarily on islands created by dredge and fill operations. We know of colonies in St. Joseph Sound, central Hillsborough Bay, and lower Boca Ciega Bay. In 1972 and 1973 we studied Laughing Gulls nesting on fill owned by the Bayway Development Corporation in lower Boca Ciega Bay, southern Pinellas County, Florida. These fill areas were created about 1960 and consist of small patches of bare ground covered with shells and coarse rubble, interspersed among the dominant saltbush (*Baccharis*), dog fennel (*Eupatorium*), and sand spurs (*Cenchrus*).

Besides Laughing Gulls, Black Skimmers (*Rynchops nigra*), Least Terns (*Sterna albifrons*), a few American Oystercatchers (*Haematopus palliatus*), and a pair of Caspian Terns (*Hydroprogne caspia*) (see Schreiber and Dinsmore, 1972) nest on these fill areas.

In 1972 we marked about 100 nests and followed their progress through hatching. In 1973 we fenced two 10 by 10 m plots with 18-in-high chicken wire (1 in hexagonal mesh); however, we were prevented from obtaining data on fledging success, as vandals ripped off the fencing. We visited the colony at intervals of about a week during each nesting season. Although more frequent visits and a longer-term study would have been desirable, the study area is now under real estate development. Thus, our 1972 and 1973 data on what was then an expanding, relatively undisturbed population probably cannot be duplicated during future nesting seasons. We believe our results provide basic information on the breeding of Laughing Gulls in Florida.

In addition to studies at the nesting colony, each year we raised two gull chicks from hatching and kept notes on their development in captivity. We have also systematically censused by age group and plumage stage the Laughing Gulls throughout the year at several localities in the Tampa Bay region. These censuses and certain other data were gathered from 1969 to 1973.

SIZE OF THE COLONY

In 1972, we estimated the number of nests by the random pairs method used by botanists (Cottam and Curtis, 1956). This method gave an estimate

of 10,000–12,000 nests for the largest nesting area. On other areas where nests were more patchy in distribution, our sample counts indicated several thousand pairs were present. Overall we estimate a minimum of 15,000 pairs in 1972, and we believe that the population was at least as large in 1973.

ANNUAL CYCLE

Based on partial data for 1969–1971 and more detailed information for 1972 and 1973, the outline of the annual plumage and nesting cycle of Laughing Gulls in the Tampa Bay region is as follows:

January.—Most of the Laughing Gulls present are adults in winter plumage, rather than first-year birds. Some adults are just starting to obtain the black hood. On 26 January 1969 only two of 50 adults had full black hoods, the earliest we have observed these.

February.—By the end of February many adults start obtaining hoods. On 12 February 1970, none of 39 adults had hoods; on 9 February 1973, 12 of 25 had hoods, and by 23 February 1973, 61 of 259 gulls had hoods. On 13 February 1970 a few gulls had gathered and were courting on the beach near the nesting colony, the earliest date we have noted this behavior.

March.—By the end of March most adults have hoods, and courtship behavior is common near the nesting colony. On 19 March 1972 hundreds of black-hooded gulls were in the vicinity of the nesting areas, sitting on the water, flying over the colony, calling and courting; nest building had not started. On 4 March 1973, over 1,000 adults, nearly all black-hooded, were in a similar state of courtship activity. As a sample, 34 of 44 gulls on 2 March 1973 had hoods, while 73 of 74 birds had hoods in the same locale on 23 March 1973.

April.—Most gulls are concentrated near the nesting areas, and fewer gulls are evident in roosting or loafing areas used by wintering birds. Virtually all adults have full hoods. On 20–22 April 1972 and 1973 hundreds of gulls were building nests at the Bayway colony. Few nests were completed or contained eggs.

May and June.—These months are the height of the breeding season for Laughing Gulls in the Tampa Bay region (Table 1). It is apparent that for the four years for which we have any data, the peak of egg-laying typically occurred in the first week of May; in 1973 it was delayed about one week. Many clutches in the first week of May have only one or two eggs; by the second week of May most have the complete three egg clutch. The earliest date we have seen chicks is 14 May, and the fourth week of May is typically the peak of hatching. By mid-June some young are able to fly short distances, and by late June most spend the day away from their natal territories resting on the beach adjacent to the colony and are capable of flight. The last nests

TABLE 1
CONTENTS OF LAUGHING GULL NESTS ON VARIOUS DATES IN FOUR NESTING SEASONS

| Date checked | Nests checked | Percent ¹ of nests containing | | | | | |
|--------------|---------------|--|----|-----|---|---------------------|-------------|
| | | Eggs | | | | Egg(s) and chick(s) | Chicks only |
| | | 1 | 2 | 3 | 4 | | |
| 1969 | | | | | | | |
| 8 May | 184 | 10 | 22 | 68 | 0 | 0 | 0 |
| 1970 | | | | | | | |
| 9 May | 66 | 6 | 21 | 73 | 0 | 0 | 0 |
| 17 May | 106 | 6 | 19 | 75 | 1 | 0 | 0 |
| 1972 | | | | | | | |
| 1 May | 47 | 26 | 26 | 49 | 0 | 0 | 0 |
| 2 May | 51 | 18 | 29 | 53 | 0 | 0 | 0 |
| 7 May | 54 | 9 | 20 | 70 | 0 | 0 | 0 |
| 10 May | 43 | 0 | 14 | 86 | 0 | 0 | 0 |
| 14 May | 161 | 6 | 25 | 68 | 0 | 1 | 1 |
| 18 May | 41 | 2 | 15 | 68 | 0 | 15 | 0 |
| 21 May | 51 | 0 | 20 | 53 | 0 | 16 | 12 |
| 23 May | 338 | 5 | 38 | 24 | 0 | 22 | 12 |
| 30 May | 23 | 0 | 0 | 0 | 0 | 9 | 91 |
| 1973 | | | | | | | |
| 14 April | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 April | 2 | 0 | 0 | 100 | 0 | 0 | 0 |
| 29 April | 24 | 29 | 50 | 21 | 0 | 0 | 0 |
| 4 May | 126 | 20 | 34 | 46 | 0 | 0 | 0 |
| 5 May | 94 | 17 | 29 | 54 | 0 | 0 | 0 |
| 12 May | 101 | 13 | 39 | 49 | 0 | 0 | 0 |
| 17 May | 252 | 9 | 38 | 50 | 0 | 2 | <1 |
| 19 May | 144 | 9 | 44 | 38 | 0 | 8 | 1 |
| 25 May | 148 | 11 | 39 | 18 | 0 | 15 | 18 |
| 31 May | 84 | 7 | 46 | 12 | 0 | 17 | 18 |
| 10 June | 32 | 25 | 25 | 3 | 0 | 16 | 31 |

¹ May not equal 100 percent because of rounding.

with eggs were found on 27 June 1972 and 22 June 1973. In 1973, with delayed nesting, on 22 June no young were capable of flight, although some were gathered on the beach. In late June the post-nuptial molt of adults is underway, as hundreds of feathers lie scattered around the colony.

On 30 May 1973, while nesting was in full swing at the Bayway colony, a count at nearby Tampa revealed 79 adults and 187 one-year-old birds, indicating the presence of some non-breeding birds in the region.

July.—Most young fledge in July. During the day thousands line the beach, most can fly at least a few hundred yards, and a few move some distance

from the colony. Molt in adults continues, and by late July black hoods are mottled with some white feathers on the lores.

August.—The number of birds at the colony decreases rapidly, so that by the end of the month it is virtually deserted. The movement of the birds-of-the-year away from the colony is especially marked, these comprising only 10 percent of 330 gulls counted there on 22 August 1972. Most adults had black and white speckled heads, the only ones with full black hoods being individuals remaining at nest sites. Further data on the exodus of gulls from the colony and the molt of adults comes from a count made in Tampa on 20 August 1973: 124 adults, 10 birds-of-the-year, and 3 one-year-old birds in a sample of 137. Only one of the adults had a full black hood, 88 had lost part or most of the hood, and 35 were in winter plumage. By late August most birds-of-the-year were growing the gray mantle feathers of their first winter plumage.

September.—Both adults and birds-of-the-year continue their molt. By the end of September most adults have the winter head plumage: only three of 349 adults counted on 28 September 1973 still had part of the hood. On that same date 13 of 53 birds-of-the-year still had an appreciable amount of brown on their mantle, and the other 40 had a gray mantle.

October.—The molts are completed essentially in October. Only 10 of 173 gulls near the nesting colony on 14 October 1973 were birds-of-the-year, all with a gray mantle: all adults had winter plumage.

November and December.—Thousands of Laughing Gulls winter in the Tampa Bay region, congregating especially around two dumps 12 miles north of the nesting colony. Virtually all gulls are in the winter plumage. Inexplicably, one adult seen in Tampa on 16 November 1973 had almost a full black hood.

While the total population may not increase in winter in the Tampa Bay region, the species is certainly more widely dispersed throughout the region, being common in parking lots, residential areas, and shopping centers, as well as in its natural saline habitats. In the period March–August gulls are not common in the more urban habitats. The local breeding population probably is augmented by wintering gulls from other areas, but we have no band recovery information to document winter movement. The recovery of some Laughing Gulls from South Carolina in Florida in winter (Forsythe, 1972) indicates one potential source of these birds.

NESTS AND NEST PLACEMENT

Bongiorno (1970) discussed in detail nest site placement in Laughing Gulls. In the Bayway colony the gulls nest on dry land, both in open areas with scattered vegetation and in areas with thick vegetation. Nests are notice-

ably more clumped in areas with some vegetative cover than in areas of only low ground cover. Two to four pairs often nest within centimeters of each other, if each of the nests is backed by a clump of *Baccharis* or *Eupatorium*. Apparently the plants visually isolate the birds (Burger, 1972). Such clumping never occurs on areas with only low ground cover. Based on 62 measurements made in 1972, the average distance between nests is 195 cm.

The nest itself is a low cup-shaped structure made of plant material, much of it from dead annuals from the previous year's growth. Outside diameters of 13 nests average 28 cm and inside diameters 16 cm. The nests rapidly disintegrate after the eggs hatch, so that by late July little of them is evident in the colony. In 1973 in particular, thick vegetation covered the nesting areas by late July. As July and August are months of heavy rainfall in the Tampa Bay region, it seems likely that this precipitation and the abundant supply of nutrients from the guano trigger the heavy growth.

CLUTCH SIZE

Our best information on clutch size comes from 94 clutches that we marked and followed closely in 1972. Seventy-eight of the clutches had three eggs and 16 had two, for an average of 2.8. Additional eggs may have been laid and lost from two egg clutches without our knowledge. Adults have three brood patches and we suspect that three eggs is the optimal usual clutch of this species. Of 17 nests marked in 1973, 13 had three eggs and four had two, for an average of 2.8.

EGG SIZE AND FLOTATION

On 7 May 1972 we obtained the following measurements from 49 eggs:
length: \bar{x} 52.6 mm, S.D. 2.4, range 47.1–58.9;
width: \bar{x} 37.8 mm, S.D. 1.1, range 34.8–40.3.

Bent (1921) gives similar results from 69 eggs: mean length 53.3 mm, range 48.5–62.0; mean width 38.5 mm, range 30.5–42.0.

Schreiber (1970) and Hays and LeCroy (1971) have described the flotation characteristics of three species of larid eggs. We were able to establish an aging scale for Laughing Gull eggs using this technique (Table 2).

HATCHING SUCCESS

In 1972 we obtained information on the hatching success of 154 eggs in 55 nests (Table 3). All eggs listed as not hatching were addled or remained in nests at least 7 days after the expected hatching date. Eggs that disappeared at about the time they were expected to hatch were placed in a questionable category. Many may have hatched, with the chicks simply leaving before we revisited the nest. As we were mainly interested in the number of addled

TABLE 2
FLOTATION CHARACTERISTICS OF LAUGHING GULL EGGS

| Age of egg (days) | Floating characteristics |
|----------------------|---|
| Day of laying | Long axis horizontal and egg resting on bottom of container. |
| Day 1-2 | Large end of egg raised slightly with long axis of egg tilted upward at angle of 5-20°. |
| Day 4-5 | Angle of long axis of egg about 45°. |
| Day 7-10 | Angle of long axis of egg about 80-90°. |
| Day 11 | Egg floats vertically free from bottom of container. |
| Day 16-18 | Egg floats on surface of water with area less than 5 mm in diameter exposed, egg bobs deeply when released. |
| Day 19-21 | Over 5 mm diameter area exposed; as greater area exposed, the long axis of egg approaches 20-30° from horizontal. |
| Day 22 | Most eggs cracked or pipped with a few hatched by this date. |
| Day 23-24 | Most eggs hatched. |
| Day 25 | All eggs hatched. |

or infertile eggs, we included all eggs that were cracked or pipped in the hatched category. As can be seen, only six percent of the eggs definitely did not hatch, and a minimum of 76 percent of the eggs did hatch. Although a somewhat higher percentage of eggs in two egg clutches were known to have hatched, this may be due to our method of collecting the data rather than there being a real difference.

GROWTH AND DEVELOPMENT

Table 4 summarizes the major growth and development parameters of four Laughing Gull chicks raised in captivity in 1972 and 1973. These chicks were taken from the nest while still damp or in pipped eggs. They were fed a diet consisting primarily of fish, shrimp, table scraps, and Purina Dog Chow. We were unable to compare our diet with the natural Laughing Gull diet, and we do not have a good series of measurements of known-aged wild

TABLE 3
HATCHING SUCCESS OF LAUGHING GULL EGGS IN 1972

| Clutch size | No. nests | No. eggs | No. hatched | No. not hatched | Questionable |
|-------------|-----------|----------|-------------|-----------------|--------------|
| 2 | 11 | 22 | 19 (86%) | 1 (5%) | 2 (9%) |
| 3 | 44 | 132 | 98 (74%) | 8 (6%) | 26 (20%) |
| Totals | 55 | 154 | 117 (76%) | 9 (6%) | 28 (18%) |

TABLE 4

SUMMARY OF THE MAJOR GROWTH AND DEVELOPMENT PARAMETERS OF FOUR LAUGHING GULLS RAISED IN CAPTIVITY¹

| | Hatching | Asymptote | Age asymptote reached | Adults ² |
|--------------|----------|------------|-----------------------|---------------------|
| Culmen | 14-15 mm | 33-34 mm | 42-44 days | 35-43 mm |
| Tarsus | 27-28 mm | 55-56 mm | 26-28 days | 47-60 mm |
| Wing (chord) | 18-20 mm | 310-315 mm | 55± days | 300-327 mm |
| Weight | 30-33 g | 310 g | 25± days | 182-360 g |

¹ Egg tooth gone at 6-7 days, young begin major loss of down at 20 days.² Based on 16 collected in the Tampa Bay region (specimens now at the University of South Florida and University of Tampa).

pulli for comparison. Based on our field observations, we believe that the asymptotic measurements and the age at which they are attained reflect the natural growth pattern of wild Laughing Gulls. The tarsi of the young are slightly longer than those of most museum specimens of adults, probably reflecting their fleshy and fluid-filled condition prior to fledging. The basic pattern of growth illustrated here for the Laughing Gull is very similar to that found in other gull species (e.g., Schreiber, 1970; Smith and Diem, 1972; Ricklefs, 1973).

MOLT

By mid-June in both 1972 and 1973 the molted feathers of adults littered the nesting area. On each of our visits to the colony in June, July, and August, we gathered all the freshly molted primaries in one portion of the colony. We compared the molted feathers with a known set of primaries to determine the primary number of each molted feather. These data are presented in Table 5, along with the weighted average molt for each date. These show a regular procession of molt from the inner to outer primary. The scarcity of outer primaries in our sample probably indicates that these are shed late in the season, after the gulls no longer frequent the colony. The timing of the molt for early 1973 is somewhat behind 1972, but by early August the two are similar.

FUTURE OF THE TAMPA BAY POPULATION

Currently, the Tampa Bay and especially the Bayway populations of Laughing Gulls appear to be thriving. The gulls have adapted well to a man-made situation by feeding in dumps and nesting on fill areas. On the other hand, automobiles and electric power lines annually kill many birds-of-the-year along the edge of the colony, and other parts of the colony are

TABLE 5
MOLT OF THE PRIMARIES BY LAUGHING GULLS AS DETERMINED BY MOLTED FEATHERS

| Date | Total feathers | Primary number | | | | | | | | | | Weighted average |
|-----------|----------------|-----------------|----|----|----|----|----|----|---|---|----|------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| 1972 | | | | | | | | | | | | |
| 30 June | 137 | 23 ¹ | 18 | 10 | 8 | 21 | 15 | 4 | - | 1 | - | 3.58 |
| 23 July | 130 | 7 | 9 | 24 | 29 | 12 | 3 | 12 | 4 | 1 | - | 4.08 |
| 3 August | 105 | 1 | - | 12 | 32 | 21 | 24 | 6 | 3 | 1 | - | 4.77 |
| 1973 | | | | | | | | | | | | |
| 15 June | 47 | 70 | 23 | - | - | 4 | 2 | - | - | - | - | 1.51 |
| 22 June | 30 | 53 | 33 | 7 | - | 3 | 3 | - | - | - | - | 1.77 |
| 12 July | 202 | 19 | 32 | 32 | 12 | 4 | - | - | 4 | - | - | 2.51 |
| 14 July | 161 | 29 | 36 | 23 | 6 | 5 | - | 1 | 1 | - | - | 2.38 |
| 5 August | 45 | - | - | 4 | 31 | 29 | 24 | 11 | - | - | - | 5.07 |
| 12 August | 46 | - | - | - | 22 | 37 | 26 | 11 | 2 | 2 | - | 5.41 |
| 19 August | 36 | 3 | 3 | 3 | 8 | 25 | 31 | 28 | - | - | - | 5.53 |

¹ Percentage of each indicated primary found on that date; may not total 100 percent because of rounding.

extensively disturbed by motorcyclists, picnickers, and other forms of human intrusion. Portions of the Bayway colony already have been bulldozed and the rest is threatened by development in the near future. Other planned development threatens virtually all suitable nesting sites in the Bayway area. Obviously, to assure the gull's continued survival in the region, a few suitable isolated areas, preferably islands, free of human disturbance from March through August, must be established. Increased human population and recreational activity in the region will make such sites rarer in the future. It will be especially interesting to see if the gulls continue to attempt to nest on traditional nesting sites, even after they are developed for such uses as golf courses.

SUMMARY

The breeding biology and annual cycle of Laughing Gulls in the Tampa Bay region are outlined. Wintering adults begin obtaining their black hood in February, and by March the gulls begin occupying the breeding areas. Courtship and nest building occur in April, and by early May the first eggs are laid. The usual clutch is three eggs, and incubation usually takes 23-24 days. A flotation technique was used to determine the incubation stage of eggs. About 75 percent of the eggs hatch, and fledging success appears high—judging from the thousands of birds-of-the-year present in late June. Adults begin their post-nuptial molt in June, and the molted feathers are present in the colony through July and August. Dispersal from the colony starts in July, and by mid-August most adults and birds of the year have left the breeding sites. Adults begin molting their hood in July, and by September virtually all are in winter plumage. In August and September birds-of-

the-year rapidly molt from the basically brown juvenal plumage into their first winter plumage. Large numbers of Laughing Gulls remain in the region during the winter. Nesting populations are thriving, but are threatened by development.

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INSECTICIDE RESIDUES IN WHITE PELICAN EGGS FROM UTAH

FRED L. KNOPF AND JOSEPH C. STREET

In 1972, we collected eggs of White Pelicans (*Pelecanus erythrorhynchos*) from Gunnison Island, Great Salt Lake, Utah, to be analyzed for insecticide residues. These analyses were performed to obtain information on a regional population of pelicans not previously surveyed for such residues and to provide background information for a study of reproductive success of the species in Utah.

METHODS

Twenty eggs of White Pelicans were collected from Gunnison Island on each of five days (15, 20, 30 April and 12, 24 May), spaced through the nesting period. On each date, eggs were taken from only those nests with incomplete clutches (full clutch size is 2), i.e. one egg. Thus, each egg collected represented the first laid in the clutch, and had not undergone substantial incubation and possible alteration of eggshell calcium (see Rothstein, 1972). Collected eggs were replaced in the nest with an egg from a 2 egg nest to minimize disturbance to any one nest. Collected eggs were individually wrapped in aluminum foil and immediately frozen.

All eggs were sectioned, and yolk samples were removed while the eggs were still frozen. From each of the five collections, 11 yolk samples were selected at random to be analyzed by electron-capture gas chromatography. Each yolk sample was desiccated with anhydrous sodium sulfate, the dried mass extracted five-times with hexane (glass distilled Skelly Solve B), and the extracts were concentrated over steam in a modified Kudena-Danish assembly. The concentrated extract was purified by chromatography on a deactivated Florisil column, with the residues collected in a single fraction eluted with 20 percent dichloromethane in hexane.

GLC analysis of the reconstituted, purified extract was performed using a Tracor MT-220 instrument equipped with Ni⁶³ electron capture detector. Residues sought included dieldrin, DDD (p,p'-), and DDE (p,p'-). Spot checking for PCB residues yielded negligible to trace quantities of these compounds in the samples. No effort was made to separate the trace PCB residues from dieldrin and DDD, the values of which may therefore be biased upwards in some cases by PCB components. DDE values were not subject to PCB interference.

Eggshells, including shell membranes, were measured for thickness using a Starrett No. 1010 micrometer. Eight lateral readings, taken midway between the caps, were averaged to give a mean thickness value for each shell.

In 1972, an estimated 5,000 to 5,200 White Pelicans nested on Gunnison Island. The first birds began laying about 1 April, and 1,010 nests (40 percent of the population) contained a complete clutch of eggs prior to our initial collection of eggs on 15 April. Approximately 95 nests (4 percent) were begun after the last collection date. Thus, collected eggs did not entirely span the laying period of this pelican population.

RESULTS

Measurable quantities of organochlorine residues were detected in all 55 egg yolks analyzed. Residue levels ranged from 0.50 to 9.88 ppm (parts per million, wet weight) dieldrin, 0.52 to 16.79 ppm DDD, and 2.01 to 57.39 ppm DDE. Mean (\pm standard error) residue levels of each compound were: 3.64 ± 0.46 ppm dieldrin, 3.70 ± 0.31 ppm DDD, and 13.62 ± 1.46 ppm DDE.

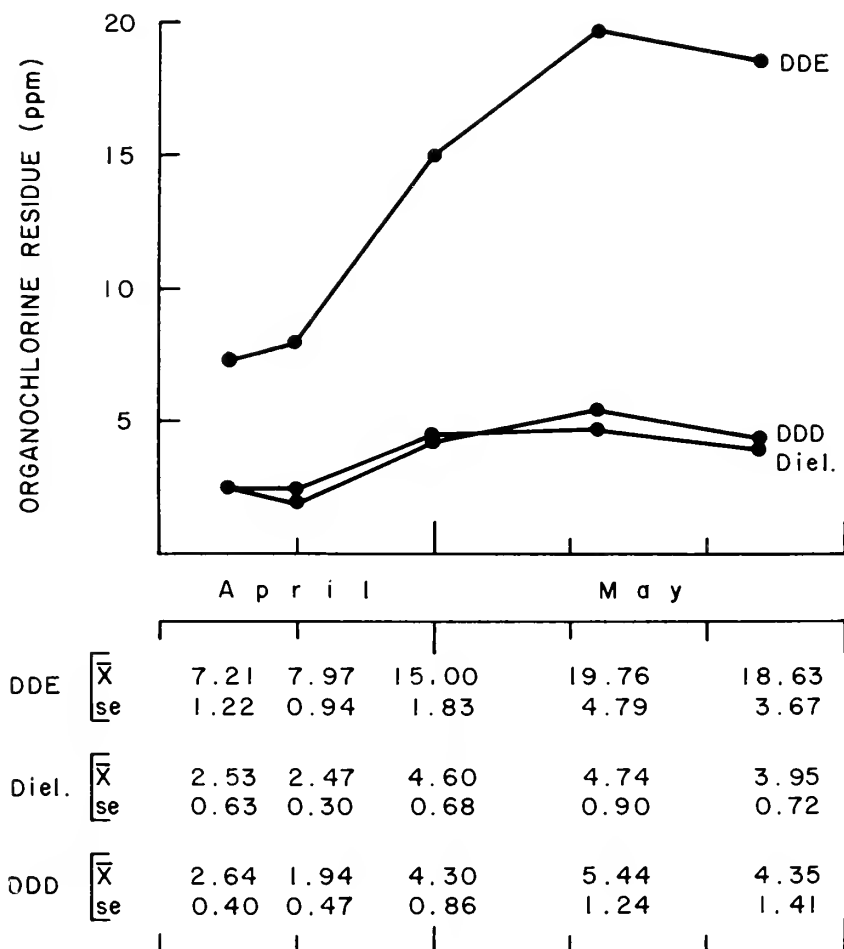


FIG. 1. Relationship between organochlorine residues in egg yolk and date of egg-laying in White Pelicans. Plotted values represent the mean of 11 yolks analyzed separately.

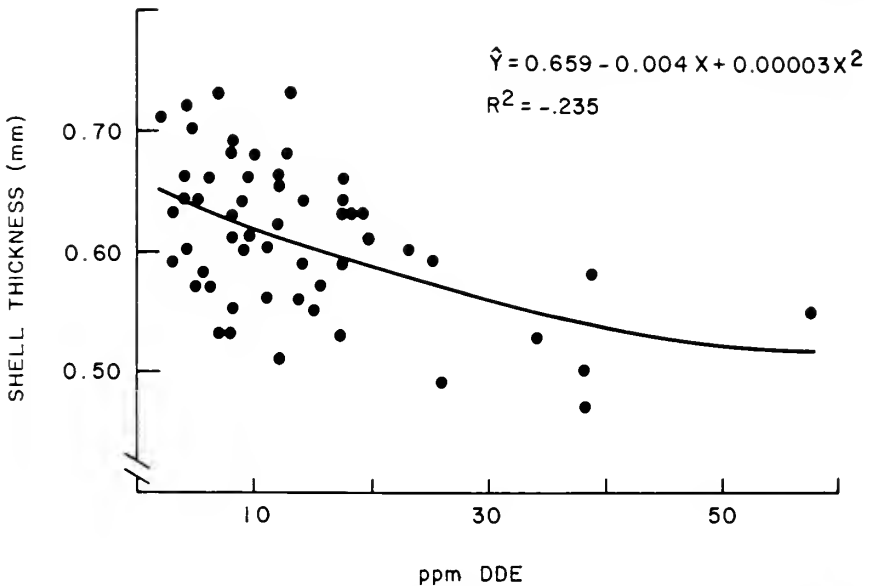


FIG. 2. Relationship between shell thickness and DDE residues in yolks of White Pelican eggs.

Mean levels of total insecticide residues in the yolk varied significantly ($F = 4.69$, $P < 0.01$) between the five collection dates (Fig. 1). Greater total insecticide loads in eggs from the later collections reflected significant increases in levels of dieldrin ($F = 2.61$, $P < 0.05$) and DDE ($F = 4.03$, $P < 0.01$). Increases in mean levels of DDD were not significant ($F = 2.13$, $P > 0.05$). The greatest one-step increase in residue levels occurred between 20 and 30 April, when mean concentrations of each residue approximately doubled. Between 12 and 24 May mean residue levels decreased slightly, but such declines were not significant.

Based upon collections from many regions of central North America, normal (pre-1940) shell thickness for White Pelican eggs, with egg membranes, is 0.686 mm (Anderson et al., 1969). Shell thickness of the 100 eggs that we collected in 1972 was 0.620 ± 0.0063 mm, the difference between the pre-1940 shells and the Gunnison Island shells being significant ($t = 6.86$, $P < 0.001$). Shell thickness of the Gunnison Island eggs decreased with increasing levels of DDE in the yolk (Fig. 2).

DISCUSSION

Some of the highest levels of insecticide residues reported in avian eggs have been in those of Brown Pelicans (*P. occidentalis*) and Double-crested

Cormorants (*Phalacrocorax auritus*) (Anderson et al., 1969; Keith et al., 1970; Gress et al., 1973; Jehl, 1973). However, residue levels in eggs of the White Pelican have remained comparatively low throughout North America (Keith, 1966b; Anderson et al., 1969; Vermeer and Reynolds, 1970; Greichus et al., 1973). Our data represent some of the first available for a Rocky Mountain population of White Pelicans and indicate that eggs of Utah birds contain levels of organochlorine residues comparable to those in eggs from other regions. The seemingly higher values in our study reflect yolk-only analyses, versus whole-egg analyses performed in the other surveys. For comparative purposes, yolk-only residue levels can be reliably converted to whole-egg values by multiplying percent yolk of total egg weight (without shell) by the wet weight residue level observed in the yolk (D. W. Anderson, pers. comm.). Expressed as whole-egg values, mean residue levels observed in Utah eggs were 0.78 ppm dieldrin, 0.79 ppm DDD, and 2.90 ppm DDE. Keith (1966b) reported mean levels of 0.20 ppm dieldrin, 0.67 ppm DDD, and 1.48 ppm DDE in eggs from northern California. Greichus et al. (1973) found 0.10 ppm dieldrin, 0.13 ppm DDD, and 2.07 ppm DDE in South Dakota. Eggs from many regions of central North America averaged 1.90 ppm DDE in 1965 (Anderson et al., 1969), while eggs collected from 16 colonies in Alberta and Saskatchewan in 1969 averaged between 0.05 and 0.38 ppm dieldrin and 0.83 and 4.76 ppm DDE (Vermeer and Reynolds, 1970).

We are uncertain whether the organochlorine residues observed in the pelican eggs were acquired in northern Utah. Local applications of DDT for large-scale insect abatement programs were illegal in 1972 and probably did not occur the preceding three to four years, according to R. Roberts (pers. comm.), Extension Entomologist, at Utah State University. A 1971 survey (Smith et al., 1974) of many Utah wildlife species found only trace residue levels in carp (*Cyprinus carpio*), the principal food item of White Pelicans in Utah (Behle, 1958:111). On the other hand, Keith (1966a) found some of the highest DDE levels reported for any marsh system yet studied at Tule Lake, California, and those levels persisted six years after DDT applications there were terminated (J. O. Keith, pers. comm.). Conceivably, localized areas of cycling high residues may still be present in some of the marshes of northern Utah.

The higher mean residue loads in eggs laid late in the nesting season probably did not reflect a cause-and-effect relationship between the residue level in the tissues of an adult and the time it laid the initial egg. Many eggs laid in May contained residue levels comparable to those in eggs laid in mid-April. In experimental studies, Jeffries (1967) and Peakall (1970) found an abnormal delay between the time of pair formation and laying of the initial egg in Bengalese Finches (*Lonchura striata*) and Ring Doves (*Streptopelia*

risoria) fed DDT in the diet. Although we were unable to determine exactly when pairing occurred in White Pelicans, all birds laid the first egg about five days after selecting a nest site. Pelican numbers on Gunnison Island increased continually throughout the breeding season, indicating that birds breeding late probably also arrived on the breeding grounds late.

The higher residue levels in eggs laid late in the season may reflect the presence of first-time breeders. Younger birds of many species breed later in the reproductive season than older birds (Lack, 1966). We are puzzled as to why younger pelicans would be carrying greater residue loads in the body tissues. Perhaps younger birds feed in those segments of the habitat containing higher levels of insecticide contamination, e.g. sewer outlets, which is suggested in the case of Brown Pelicans (J. R. Jehl, pers. comm.). An alternative explanation is that birds arriving late on the breeding grounds experience a greater exposure to insecticide residues just prior to egg formation. Such exposure would result from local applications of insecticides during the nesting season, or an increased rate of transfer through the food chain of those residues already in the marsh system. Admittedly, these are speculations. Causes for the three-fold increase in DDE residues (Fig. 1) merit investigation. The design of egg collecting in future insecticide surveys of avian populations should consider the possible occurrence of a similar pattern of increasing levels through time.

Renesting birds tend to lay eggs with lower residue loads than birds nesting for the first time in a season (Ludwig and Tomoff, 1966; Anderson et al., 1969). In our study, the slight decrease in mean residue levels between 12 and 24 May may be due to the presence of renesting pelicans in the latter collection.

The higher residue levels in late-nesting birds did not appear to have a significant impact upon the reproductive success of the pelican population. Residue levels were low in the 20 April collection, at which time 60 percent of the pelicans had laid. During the egg collections only one of 791 nests checked contained a broken egg, and that shell did not appear thin. Observations in 1973 (unpublished data) indicate that the incidence of egg mortality, especially through nest desertion, is low among birds breeding in April but approaches 50 percent among those breeding in June. Such mortality may reflect the inexperience of birds breeding for the first time, rather than the presence of higher insecticide loads in individuals.

SUMMARY

White Pelican eggs were collected at the time of laying on Gunnison Island, Great Salt Lake, Utah. Egg yolks were analyzed for the presence of dieldrin, DDD, and DDE, and shells were measured for thickness. Wet weight concentrations of residues averaged 3.64 ± 0.46 ppm dieldrin, 3.70 ± 0.31 ppm DDD, and 13.62 ± 1.46 ppm DDE. These levels

are comparable to those reported for the species from other regions of North America. Concentrations of dieldrin and DDE were significantly higher in eggs laid late in the reproductive season, but reasons for this are not known. Our data suggest that the residue levels observed in the eggs of free-living avian populations may depend on the time of collections.

Shells of pelican eggs were significantly thinner than for pre-1940 eggs. Shell thickness of an egg decreased with increasing levels of DDE in the yolk.

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ACCEPTED 12 JUNE 1974.

WILSON ORNITHOLOGICAL SOCIETY ANNUAL MEETINGS

- | | |
|------------------------------------|---|
| 1st 1914 Chicago, Illinois | 29th 1947 Columbus, Ohio |
| 2nd 1914 Chicago, Illinois | 30th 1949 Madison, Wisconsin |
| 3rd 1915 Columbus, Ohio | 31st 1950 Jackson's Mill, West Virginia |
| 4th 1916 Chicago, Illinois | 32nd 1951 Davenport, Iowa |
| 5th 1917 Pittsburgh, Pennsylvania | 33rd 1952 Gatlinburg, Tennessee |
| 6th 1919 St. Louis, Missouri | 34th 1953 Cheboygan, Michigan |
| 7th 1920 Chicago, Illinois | 35th 1954 Cape May, New Jersey |
| 8th 1921 Chicago, Illinois | 36th 1955 Stillwater, Oklahoma |
| 9th 1922 Chicago, Illinois | 37th 1956 Buffalo, New York |
| 10th 1923 Cincinnati, Ohio | 38th 1957 Duluth, Minnesota |
| 11th 1924 Nashville, Tennessee | 39th 1958 Wheeling, West Virginia |
| 12th 1925 Kansas City, Missouri | 40th 1959 Roekland, Maine |
| 13th 1926 Chicago, Illinois | 41st 1960 Gatlinburg, Tennessee |
| 14th 1927 Nashville, Tennessee | 42nd 1961 Huntsville, Ontario, Canada |
| 15th 1928 Ann Arbor, Michigan | 43rd 1962 Lafayette, Indiana |
| 16th 1929 Des Moines, Iowa | 44th 1963 Charleston, South Carolina |
| 17th 1930 Cleveland, Ohio | 45th 1964 Kalamazoo, Michigan |
| 18th 1931 New Orleans, Louisiana | 46th 1965 Sylvan Lake, South Dakota |
| 19th 1932 Columbus, Ohio | 47th 1966 University Park, Pennsylvania |
| 20th 1934 Pittsburgh, Pennsylvania | 48th 1967 Crawford Notch, N. Hampshire |
| 21st 1935 St. Louis, Missouri | 49th 1968 Carbondale, Illinois |
| 22nd 1936 Chicago, Illinois | 50th 1969 Williamsburg, Virginia |
| 23rd 1937 Indianapolis, Indiana | 51st 1970 Fort Collins, Colorado |
| 24th 1938 Ann Arbor, Michigan | 52nd 1971 Dauphin Island, Alabama |
| 25th 1939 Louisville, Kentucky | 53rd 1972 Cape May, New Jersey |
| 26th 1940 Minneapolis, Minnesota | 54th 1973 Chapel Hill, North Carolina |
| 27th 1941 Urbana, Illinois | 55th 1974 Cheboygan, Michigan |
| 28th 1946 Omaha, Nebraska | |

AN ANALYSIS OF NEST BOX USE BY PURPLE MARTINS, HOUSE SPARROWS, AND STARLINGS IN EASTERN NORTH AMERICA

JEROME A. JACKSON AND JAMES TATE, JR.

In eastern North America the Purple Martin (*Progne subis*) now nests almost exclusively in houses provided by man. Recognizing this dependency on and popularity with man, Jackson initiated a survey of martin populations in Mississippi in 1971. The purposes of the survey were to monitor population fluctuations of the species over a period of years and to determine the habitat characteristics that favor a successful martin colony. The survey met with such overwhelming response from the general public that it was soon expanded to include all of eastern North America. The questionnaires that were distributed also asked for information relating to the population biology of other hole-nesting species, particularly House Sparrows (*Passer domesticus*) and Starlings (*Sturnus vulgaris*), that compete with martins for nest sites. This paper is an analysis of the response of volunteer cooperators to two questionnaires that were distributed for the 1971 breeding season. The previous published surveys of Purple Martin populations by Bartel (1947, 1959), Mayfield (1964, 1969), and Hunter (1967) were on a smaller scale within small geographic areas, and they considered population numbers without regard for nest site characteristics.

THE QUESTIONNAIRE AND ANALYSIS

The initial single page questionnaire included the following questions:

1. We have (*number*) martin house(s) and (*number*) gourds for martins. These provide a total of (*number*) nest compartments.
2. At the present time (*day month year*) we have the following actual or approximate number of individuals occupying our nest compartments: Purple Martins (*number*), House Sparrows (*number*), Starlings (*number*), Other (Specify) (*number*).
3. Our martin house and/or gourds are approximately (*number*) feet above the ground.
4. The area immediately surrounding our martin house and/or gourds (within about 50 ft.) (Circle one): 1) is a lawn or pasture with few small shrubs; 2) is a lawn or pasture with one or more small trees; 3) is a lawn or pasture with one or more large trees; 4) Other (Specify).
5. Our martin house and/or gourds are approximately (*number*) feet from the nearest building.

This questionnaire was freely distributed to any potential respondent, and was completed by 1067 persons from 32 states, the District of Columbia, and five Canadian provinces. These areas and numbers of respondents were as follows: Alabama (5), Arkansas (47), Connecticut (8), Delaware (1), District of Columbia (2), Florida (12), Georgia (1), Illinois (16), Indiana (3), Iowa (108), Kansas (2), Louisiana (8), Maine

(12), Maryland (11), Massachusetts (1), Michigan (11), Minnesota (18), Mississippi (592), Missouri (4), Nebraska (5), New Hampshire (1), New Jersey (14), New York (77), North Dakota (1), Ohio (10), Oklahoma (12), Pennsylvania (26), Rhode Island (1), South Carolina (7), Tennessee (9), Texas (5), Virginia (8), Wisconsin (8), Alberta (4), Manitoba (1), Nova Scotia (1), Ontario (12), Quebec (3).

The phraseology of our question relating to the number of birds using the apartments resulted in some misinterpretation and inconsistent data. We asked for the number of each species using the apartments, so that at times nestlings as well as adults were counted. Where this was apparent, these data were questioned and corrected or discarded.

For the purpose of this study, the word colony is used to refer to all of the apartments supplied by one respondent at one locality. A colony may include one or more apartment house and/or gourds. An apartment is defined as a single potential nest site, whether it is a separate unit, such as a gourd, or part of a multiple unit structure (i.e., an apartment house).

Using the data from the first questionnaire, we calculated the ratios of martins, sparrows, and Starlings per apartment. In addition, some comparisons of martin and sparrow populations and the relative use by the birds of apartments in houses and gourds in Mississippi were possible because of the large number of cooperators from that state. These ratios were compared for different geographic areas, and for differences in apartment heights, distance of apartments from the nearest building, and immediate environment of the apartments.

The second questionnaire, sent to respondents to the first, consisted of three pages relating to apartment characteristics, colony history, habitat, apartment maintenance, and apartment use by the birds. Only data for apartment houses ($N = 622$) are included here in our analysis of the second questionnaire data. Separate questionnaires were completed for each multiple-apartment house. Questions regarding the characteristics and location of the house included the following:

1. We have (*number*) multiple-apartment houses and (*number*) single-apartment houses or gourds.
2. The multiple-apartment house here described was first erected on the present site in (*year*).
3. There are other martin colonies within one-half mile of this one. 1. Yes 2. No.
4. This house is 1. Aluminum 2. Wood 3. Plastic 4. Fiberglass 5. Ceramic 6. Other.
5. The outside of this house is basically 1. White 2. Green 3. Brown 4. Red 5. Blue 6. Other.
6. The inside of the apartments is basically 1. White 2. Green 3. Brown 4. Other.
7. This house is in the shade 1. Only in early morning 2. Most of the morning 3. Most of the day 4. Most of the afternoon 5. Only in late afternoon 6. All of the day 7. Never in the shade 8. Other.
8. The location of this house can best be described as 1. Urban, business, or industrial area 2. Urban, residential area 3. Suburban 4. Rural 5. Other.
9. There is a lake, pond, stream, or river that can be seen from the martin house. 1. Yes 2. No.
10. There are power or telephone lines that can be seen from the martin house. 1. Yes 2. No.
11. We clean the apartments out each year. 1. Yes 2. No 3. Sometimes 4. Does not apply.

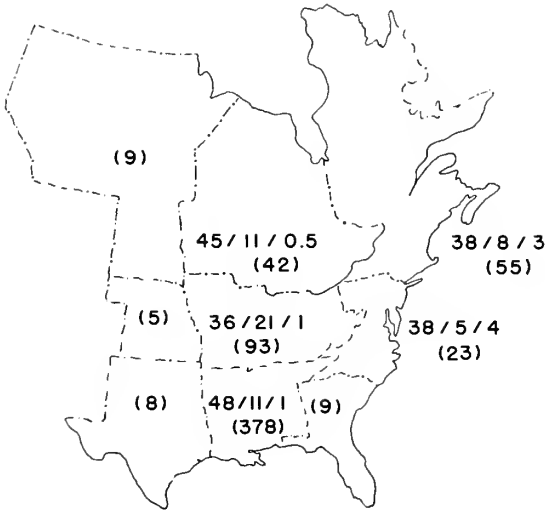


FIG. 1. Arbitrary (and a priori) division of eastern North America into nine sectors for analysis of nest box occupancy. Numbers separated by slashes are the percentages of apartments occupied by Purple Martins, House Sparrows, and Starlings, respectively. Numbers in parentheses indicate the total number of colonies from which data were received.

12. There are bushes or high shrubbery growing at the base of the pole supporting the house. 1. Yes 2. No.
21. This house is approximately (*number*) feet above the ground or water.

Data for colonies using gourds were available from too few colonies to permit meaningful statistical analysis. Rather than asking for the number of individuals using the apartments, on the second questionnaire we asked for the total number of apartments occupied by each species. Because of the small total sample size the data were grouped for analysis into nine geographic regions as indicated in Figure 1. These regions will be referred to in subsequent discussions as the northwest, north-central, northeast, west-central, central, and so on.

Using data from the second questionnaire, we calculated the percentage of apartments in each colony that were occupied by martins, sparrows, and Starlings, and compared variation in these percentages with variation in several physical and biotic parameters. Statistical comparisons of data from both questionnaires were made by using a simple analysis of variance, the sum of squares simultaneous test procedure (STP) (Sokal and Rohlf, 1969:685-687), the test for equality of two percentages discussed by Sokal and Rohlf (1969:607-608), or the method of Brandt and Snedecor (Snedecor, 1956:227-230) for comparison of sets of more than two percentages.

Sample sizes for the various data sets refer to the number of colonies or houses; percentages refer to the number of apartments occupied.

RESULTS

First Questionnaire.—One of the major findings from the first questionnaire was a statement of the relative abundance and distribution of Purple Martins. This information is given in Table 1, expressed as ratios of occupancy for each state or Canadian province from which there were five or more cooperators. In general, the number of martins per apartment is highest in southwestern Ontario along Lake Erie, along the Maine coast, and in the mid-south (Tennessee and Mississippi). The lowest ratios are from parts of the mid-west, middle Atlantic states, and Florida. An analysis of variance indicates that there is significant geographic variation in the use of apartments by martins ($p \leq 0.05$).

TABLE 1
RATIO OF MARTINS/APARTMENT FOR EACH STATE OR CANADIAN PROVINCE REPRESENTED BY
DATA FROM FIVE OR MORE COLONIES

| State or province | Total number of apartments | Total number of Purple Martins | Ratio: martins/apartment |
|-------------------|----------------------------|--------------------------------|--------------------------|
| Ontario | 232 | 363 | 1.56 |
| Maine | 310 | 360 | 1.16 |
| Tennessee | 314 | 362 | 1.15 |
| Mississippi | 13133 | 10797 | 0.82 |
| Oklahoma | 182 | 133 | 0.73 |
| Virginia | 152 | 107 | 0.70 |
| New York | 1587 | 1086 | 0.68 |
| New Jersey | 278 | 190 | 0.68 |
| Ohio | 237 | 159 | 0.67 |
| South Carolina | 124 | 80 | 0.65 |
| Arkansas | 893 | 561 | 0.63 |
| Iowa | 2592 | 1620 | 0.63 |
| Alabama | 160 | 116 | 0.63 |
| Wisconsin | 286 | 164 | 0.57 |
| Louisiana | 223 | 121 | 0.54 |
| Pennsylvania | 607 | 299 | 0.49 |
| Texas | 100 | 46 | 0.46 |
| Maryland | 217 | 96 | 0.44 |
| Illinois | 362 | 151 | 0.42 |
| Minnesota | 418 | 157 | 0.38 |
| Nebraska | 86 | 27 | 0.31 |
| Florida | 402 | 110 | 0.27 |
| Michigan | 174 | 46 | 0.26 |
| Connecticut | 322 | 48 | 0.15 |

TABLE 2
RATIO OF BIRDS/APARTMENT IN RELATION TO APARTMENT HEIGHT AND VEGETATION
WITHIN 15.2 M OF THE APARTMENTS

| | Number of colonies | Ratio of birds/apartment | | |
|-------------------------|--------------------|--------------------------|----------|-----------|
| | | Martins | Sparrows | Starlings |
| Apartment height (m) | | | | |
| 2 < 3 | 72 | 0.75 | 0.20 | 0.05 |
| 3 < 4 | 202 | 0.64 | 0.18 | 0.01 |
| 4 < 5 | 370 | 0.67 | 0.20 | 0.03 |
| 5 < 6 | 95 | 0.73 | 0.23 | 0.02 |
| 6 < 7 | 125 | 0.63 | 0.21 | 0.03 |
| 7 < 8 | 53 | 0.73 | 0.20 | 0.03 |
| Vegetation | | | | |
| A few small shrubs | 187 | 0.74 | 0.15 | 0.03 |
| One or more small trees | 366 | 0.68 | 0.20 | 0.03 |
| One or more large trees | 532 | 0.67 | 0.20 | 0.03 |

From that survey we also found the height of the apartments seems to have little effect on occupancy. Data for apartment height were grouped into six classes (Table 2), among which no significant differences were found in occupancy values for any of the species considered.

On the other hand, the distance of apartments from the nearest building seems to be important to martins, but less so to sparrows or Starlings. There were no significant differences among mean ratios of martins per apartment for distance subsets closer than 30 m from the nearest building. Apartments closer than 30 m, however, had significantly more ($p \leq 0.05$) martins (mean = 0.73 martins/apartment) than did apartments that were more than 30 m distant (mean = 0.55 martins/apartment).

Finally no significant differences were indicated in occupancy rates as related to habitat types in the vicinity of the apartments. We did note a trend toward fewer martins and more sparrows ($p \leq 0.1$) with increasing height of vegetation (Table 2), although a larger sample size and/or a refinement of the question is needed to statistically confirm the relationships.

The very large body of data from Mississippi makes it possible to compare colonies using gourds, houses, or both. From that state 592 cooperators reported 3,173 gourds and 1,046 houses with a total of 13,133 apartments available for birds. Totals of 10,797 Purple Martins, 1,754 House Sparrows, and 379 Starlings were reported nesting in these apartments. Table 3 summarizes the ratios of martins and sparrows per apartment for the three colony types (Starlings were not analyzed because of their relatively smaller number).

TABLE 3
RATIO OF MARTINS/APARTMENT AND SPARROWS, APARTMENT IN GOURDS AS
OPPOSED TO HOUSES IN MISSISSIPPI

| Colony type | Number of colonies | Martins/apartment | Sparrows/apartment |
|------------------------|--------------------|-------------------|--------------------|
| Gourds only | 73 | 1.20 | 0.07 |
| Houses only | 352 | 0.83 | 0.17 |
| Both houses and gourds | 164 | 0.66 | 0.18 |

The three ratios for martins all are significantly different ($p \leq 0.01$). The ratio of sparrows/apartment for gourd colonies is significantly less than the ratio for either colonies with houses or colonies with both houses and gourds ($p \leq 0.02$).

Comparison of the ratio of martins/apartment in house and gourd colonies in Mississippi with and without sparrows also indicates significant differences ($p \leq 0.05$). In colonies with apartment houses and no sparrows there were more martins per apartment (ratio = 1.02, $n = 122$) than in colonies without sparrows (ratio = 0.79, $n = 217$). This was also true in colonies with gourds as apartments (no sparrows: ratio = 1.36, $n = 49$; with sparrows: ratio = 0.98, $n = 21$). There were also significantly more martins in gourd colonies without sparrows than in house colonies without sparrows. The difference between house and gourd colonies with sparrows was not significant, nor was that between house colonies without sparrows and gourd colonies with sparrows.

Second Questionnaire.—Analysis of data from the second questionnaire provides more insight into the geographic variation in relative population levels and the factors influencing nest-site selection in the three species.

Analysis of the percentages of apartments used by the birds in the nine geographic sectors (Fig. 1) confirms the trends indicated by data from the first questionnaire. STP analysis reveals two non-significant subsets based on the ranked means of percentages of apartments used by martins. Occupancy is higher in the south-central than in the central region, but differences between other pairs of sectors are not statistically significant.

Significant geographic variation is also indicated in the relative use of apartments by sparrows. Two non-significant subsets were defined by STP analysis—the central sector had a significantly higher proportion of sparrows than any other area. There were no significant differences between any pair of the remaining sectors.

Analyses of the types of house (Table 4) showed higher percentage of occupancy in wooden than in aluminum houses for all three species; however,

TABLE 4
PERCENTAGE OF APARTMENTS OCCUPIED RELATIVE TO THE PHYSICAL CHARACTERISTICS
AND GENERAL LOCATION OF THE HOUSE

| | Number of | | Percentage of apartments occupied by: | | |
|---|-----------|------------|---------------------------------------|----------|-----------|
| | Houses | Apartments | Martins | Sparrows | Starlings |
| Type of house | | | | | |
| Aluminum | 224 | 2946 | 40.6 | 11.0 | 0.3 |
| Wood | 394 | 5379 | 44.1 | 12.4 | 1.8 |
| Exterior color | | | | | |
| White | 556 | 7585 | 43.9 | 11.7 | 1.0 |
| Brown | 20 | 218 | 28.4 | 16.1 | 8.3 |
| Green | 28 | 341 | 30.8 | 17.9 | 2.6 |
| Interior color | | | | | |
| White | 295 | 3798 | 43.2 | 10.2 | 1.0 |
| Brown | 282 | 3886 | 44.9 | 13.9 | 1.6 |
| Apartments clean in spring | | | | | |
| Yes | 526 | 7200 | 41.9 | 12.5 | 0.9 |
| No | 43 | 502 | 53.4 | 9.6 | 3.4 |
| Location | | | | | |
| Urban-business | 22 | 314 | 57.3 | 13.4 | 0.3 |
| Urban-residential | 253 | 3204 | 45.1 | 13.1 | 1.2 |
| Suburban | 147 | 2036 | 34.6 | 14.4 | 1.7 |
| Rural | 198 | 2791 | 45.1 | 8.6 | 1.2 |
| Water within sight | | | | | |
| Yes | 295 | 3920 | 45.6 | 10.5 | 1.4 |
| No | 324 | 4409 | 40.5 | 13.1 | 1.2 |
| Neighboring martin house | | | | | |
| Yes | 498 | 6569 | 43.9 | 13.0 | 1.1 |
| No | 121 | 1748 | 39.5 | 8.0 | 1.8 |
| Utility wires within sight | | | | | |
| Yes | 584 | 7843 | 42.6 | 12.0 | 1.3 |
| No | 36 | 502 | 47.4 | 10.4 | 0.4 |
| Shrubs at base of support pole | | | | | |
| Yes | 137 | 1910 | 43.2 | 14.8 | 1.7 |
| No | 481 | 6401 | 42.8 | 11.1 | 1.1 |

TABLE 5
PERCENTAGE OF APARTMENTS OCCUPIED IN RELATION TO THE AMOUNT OF TIME A HOUSE IS
IN THE SHADE

| | Number of | | Percentage of apartments occupied by: | | |
|--|-----------|------------|---------------------------------------|----------|-----------|
| | Houses | Apartments | Martins | Sparrows | Starlings |
| Time during which the house is shaded | | | | | |
| Never | 353 | 4934 | 43.5 | 12.2 | 1.4 |
| Always | 13 | 182 | 46.2 | 9.3 | 0.0 |
| Only late afternoon | 108 | 1466 | 45.4 | 9.4 | 1.4 |
| Most of the afternoon | 10 | 108 | 43.5 | 19.4 | 0.9 |
| Most of the day | 12 | 150 | 36.0 | 24.7 | 5.3 |
| Only early morning | 99 | 1224 | 40.1 | 12.2 | 0.7 |
| Most of the morning | 20 | 211 | 32.2 | 11.4 | 0.0 |

the difference approaches significance only for Starlings ($p \leq 0.01$). Most houses (92 percent) were painted white: thus, in spite of large differences in the average percent occupancy, sample sizes for brown and green houses are too small to prove the differences are statistically significant. The data do suggest that martins might favor white houses ($p \leq 0.2$) while Starlings favor darker ones ($p \leq 0.01$). Martins and Starlings showed no clear preference for white or dark (brown or natural wood) interiors in their apartments, but sparrows may prefer ($p \leq 0.2$) the darker colors.

Comparison of houses that were cleaned out before the beginning of the

TABLE 6
PERCENTAGE OF APARTMENTS OCCUPIED IN 1971 AS IT RELATES TO THE YEAR IN WHICH A
HOUSE WAS FIRST ERECTED

| Year house was first erected | Number of | | Percentage of apartments occupied by: | | |
|---------------------------------|-----------|------------|---------------------------------------|----------|-----------|
| | Houses | Apartments | Martins | Sparrows | Starlings |
| 1971 | 113 | 1398 | 30.0 | 10.0 | 1.4 |
| 1970 | 86 | 1165 | 43.0 | 9.7 | 1.1 |
| 1969 | 90 | 1125 | 48.4 | 11.3 | 1.3 |
| 1968 | 91 | 1160 | 42.5 | 12.8 | 1.5 |
| 1967 | 53 | 677 | 43.6 | 15.2 | 1.9 |
| 1966 | 46 | 608 | 50.5 | 14.8 | 1.6 |
| 1965 | 40 | 555 | 56.6 | 11.9 | 0.0 |
| Before 1965 | 93 | 1558 | 41.5 | 12.9 | 1.0 |

TABLE 7
THE PERCENTAGE OF APARTMENTS OCCUPIED IN RELATION TO THE NUMBER OF APARTMENTS/HOUSE

| Number of apartments/house | Number of | | Percentage of apartments occupied by: | | |
|-------------------------------|-----------|------------|---------------------------------------|----------|-----------|
| | Houses | Apartments | Martins | Sparrows | Starlings |
| 8 or fewer | 122 | 789 | 49.9 | 14.6 | 1.8 |
| 9-12 | 280 | 3284 | 41.9 | 11.6 | 0.9 |
| 13-16 | 91 | 1403 | 43.6 | 15.0 | 1.5 |
| 17-20 | 68 | 1273 | 47.8 | 8.9 | 2.1 |
| 21-24 | 46 | 1132 | 32.8 | 11.1 | 0.7 |
| 25-28 | 3 | 80 | 52.5 | 2.5 | 0.0 |

breeding season and those that were not suggests that martins might prefer to use an old nest as a base for a new one ($p \leq 0.2$). Only 43 cooperators failed to clean out their bird houses.

Analyses of the general location of houses (Table 4) show that suburban colonies had significantly fewer martins ($p \leq 0.05$) than did urban-business, urban-residential, or rural colonies. Rural martin houses tended to have fewer sparrows than did either suburban ($p \leq 0.1$) or urban-residential colo-

TABLE 8
PERCENTAGE OF APARTMENTS OCCUPIED BY SPECIFIC COMBINATIONS OF MARTINS, SPARROWS, AND STARLINGS

| Birds Present | Number of | | Percentage of apartments occupied by: | | |
|-------------------------------------|-----------|------------|---------------------------------------|----------|-----------|
| | Houses | Apartments | Martins | Sparrows | Starlings |
| No birds | 53 | 769 | 0.0 | 0.0 | 0.0 |
| Martins only | 205 | 2575 | 57.1 | 0.0 | 0.0 |
| Sparrows only | 31 | 382 | 0.0 | 20.2 | 0.0 |
| Starlings only | 6 | 88 | 0.0 | 0.0 | 20.5 |
| Martins and sparrows only | 281 | 3836 | 48.1 | 20.4 | 0.0 |
| Martins and Starlings only | 9 | 164 | 50.0 | 0.0 | 13.4 |
| Sparrows and Starlings only | 13 | 183 | 0.0 | 33.9 | 16.9 |
| Martins, sparrows, and Starlings | 24 | 375 | 50.1 | 19.2 | 9.1 |

nies. The presence of a pond, lake, or stream within sight of a house may result in a greater occupancy by martins ($p \leq 0.2$). Occupancy by sparrows was less, but not significantly so. The occurrence of another house within one-half mile had no significant effect on the percent occupancy by martins, but the increase in the percent occupancy by sparrows approaches significance ($p \leq 0.15$). The presence of utility wires within sight had no discernible effect on the percent occupancy of a house by any of the species.

The presence of bushes or other high vegetation at the base of the support pole apparently does not influence the rate of occupancy of the house by martins, but may favor occupancy by sparrows ($p \leq 0.25$). Statistical comparison of colonies that are in the shade at various times (Table 5) indicates no significant differences for any species, though some trends are suggested. Martins may prefer houses that receive morning sun, and sparrows seem to prefer houses that receive some but not afternoon sun. Larger sample sizes are needed to confirm these patterns.

The percent occupancy by martins for houses erected in 1971 (Table 6) is significantly lower ($p \leq 0.05$) than the average percent occupancy for nest boxes erected earlier. No such difference is apparent for sparrows or Starlings. Comparison of occupancy rates in relation to the number of apartments in a house (Table 7) shows no immediate pattern, though the percentage of apartments occupied by martins in houses with eight or fewer apartments is significantly greater than the value for houses with nine to 12 apartments.

Finally, a comparison of houses only occupied by specific combinations of these three species (Table 8) indicates that houses with only martins have significantly more martins than houses that also have sparrows. There were no significant differences within the sets of combinations including sparrows or Starlings.

DISCUSSION

Nest Site Preferences.—Attempts to manage game, aesthetically pleasing, or rare species have multiplied in recent years with the advent of a greater ecological awareness. The Purple Martin, however, is a species that was managed in North America even before the arrival of European man. Indians in the Southeast hung calabash gourds from trees near their villages or from poles in their corn fields. Martins accepted these nest sites and, as a result of their mobbing behavior, kept predators away from the corn and foodstuffs that were hung up to dry (Audubon, 1831; Ewan and Ewan, 1970). The early colonists substituted ceramic jugs and wooden apartment houses for gourds in attempts to attract martins. For example, Audubon (op. cit.) noted that "Almost every country tavern has a martin box on the upper part of its sign-board."

Through the years, martin houses have appeared in as many styles, shapes, and sizes as human dwellings, and a lot of generalities have been made about what will and what won't attract martins. While man has "managed" martins for centuries, the management has been based primarily on tradition, and testing of management practices has been limited to trial and error. One result of our study is that the putative nest site requirements of martins have been objectively analyzed. Such "requirements" have been enumerated many times (e.g., Wade, 1966; Layton, 1969) and generally include such things as: 1. the apartment house should be in an open area at least 8 m from the nearest tree or building; 2. the house should be on a pole 5–10 m above the ground; 3, martins need or prefer utility wires near the house; 4. a pond, lake, or stream nearby is characteristic of a preferred habitat; and 5. the apartments should be cleaned out each year.

Clark (1970) quantitatively examined the relationship between apartment characteristics and rate of occupancy by martins, but, because of her small sample size, her results are inconclusive. Our study confirms some of the suggested requirements, but refutes others. Our data do not support the contention that a martin house should be away from trees or buildings. In fact, houses within 30 m of a building seem to be preferred to those farther away. No clear preferences are shown with regard to apartment height or the presence or absence of utility wires. The contention that martins prefer water nearby is supported.

Most noteworthy is the suggestion that martins prefer apartments that haven't been cleaned out before the beginning of the nesting season. Kinney (1972) notes the use of old nests by Purple Martins, and one of our cooperators reported that the first apartments occupied by martins are always those containing old nests. Boyd (1935) points out that House Martins (*Delichon urbica*) "generally reline and use an old nest," and frequent use of old nests has been observed for the Cliff Swallow (*Petrochelidon pyrrhonota*) (Buss, 1942; Samuel, 1971) and Barn Swallow (*Hirundo rustica*) (Samuel, 1971). The potential energetic savings resulting from use of an old nest is obvious and might be expected to be selected for, though an inherent disadvantage is that old nests harbor parasites that may reduce the fecundity of the birds (Moss and Camin, 1970). From a Purple Martin management point of view we recommend that House Sparrow and Starling nests be removed and that martin nests be left, but dusted with some non-persistent miticide.

It appears that we have been trying to attract martins by following a set of guidelines that for the most part either do not influence the birds or that influence them negatively. Considering this revelation, it would seem appropriate that other management programs, particularly those involving en-

dangered species, be examined for practices that are based on tradition rather than on objective analysis of data.

First Year Occupancy of Houses by Martins.—Mayfield (1964, 1969) in a fifteen-year study of martin houses in Ohio, reported the houses as fully occupied their first year as in subsequent years. However, a reexamination of his data suggests that his sample sizes may have been too small to give statistically valid results. For the first ten years of the study (Mayfield, 1964) 18 of 32 houses had fewer martins the first year than the average for all years. A comparison of this number with the number of houses having the average or a greater number of martins indicates no significant differences ($\chi^2 = 0.50$). With five more years data (Mayfield, 1969) the differences are still not significant (21 houses with fewer than the average number of martins the first year, 15 with the average or more; $\chi^2 = 1.0$), but the increased chi square value and trend of the data suggest that only increased sample size is needed for statistical proof. In our study comparison of a large number of houses for a single year confirms the traditional suggestion that first year houses are likely to attract fewer martins. This may be because houses are frequently placed by inexperienced people on a trial-and-error basis and often moved if unused. Such a difference probably also reflects the tendency for young martins to return to the general area of the colony in which they were hatched and for adults to return to the same colony to nest year after year (Allen and Nice, 1952; Olmstead, 1955).

Competition Among Species for Nest Sites.—The data presented here suggest that Starlings are not a serious threat to the Purple Martin as a nest site competitor (though they may be a serious threat as a predator on nestlings and eggs (Flentge, 1940; Gaunt, 1959)). Kessel (1957) never found more than one pair of Starlings nesting in a multi-apartment house. She states that one male will defend an entire apartment house against other Starlings but that "once settled in his small domain . . . the starling becomes an unobtrusive neighbor" to other species. Finally, as Wade (1966) suggests and this study confirms, aluminum houses which are used widely for martins, further deter the Starling from competing with martins.

House Sparrows, unlike Starlings, will nest communally and therefore present more of a problem for martins. The relative degree to which these species have adapted to communal nesting is perhaps reflected by the average percentage of apartments they occupy in a colony. We found these figures to be 48.1 percent for martins and 20.4 percent for sparrows, and Olmstead (1955) reported similar values (50.0 percent for martins, 18.2 percent for sparrows) for a Kansas colony he studied for five years. With such a high percentage of apartments occupied by sparrows, it is not surprising that the presence of sparrows results in a significant decrease in the number of apart-

ments martins occupy. The effect of sparrows, however, may be more than a proportionate loss of potential martin nest sites. Pindar (1923) suggests that if there are only a few martins at an apartment house they may be completely repelled by sparrows. Furthermore, when there are a large number of martins such that most apartments are occupied, the male House Sparrows are likely to usurp the martins' nests and destroy their eggs (Olmstead, 1955).

Geographic variation in the relative abundance of martins, sparrows, and Starlings may be related to interspecific competition. In the central region of the eastern United States (Fig. 1), martins are at their lowest, sparrows at their highest, and Starlings at a low relative abundance. In the northeast and east-central regions martins are at a low, sparrows at their lowest, and Starlings at their highest levels. In the south-central region martins are at their highest, and sparrows and Starlings are both at low levels. Levels of all three species may be reduced in the northern sections as a result of some competition with Tree Swallows (*Iridoprocne bicolor*), which are known to nest in martin houses (Tate, 1963; observations reported by participants in this study).

Additional limiting factors may contribute to the regional differences in relative abundance of the species. Climate during the breeding season (hence supply of flying insects) is a known limiting factor for martins (Horton, 1903; Tate, 1972). Amount of land under cultivation for grain crops or number of head of granivorous livestock (hence food supply) may limit sparrows. Suggestive of this is the fact that the central region, where sparrows are relatively most numerous, is well defined (Jones, 1972) as the major area of corn and hog production in North America. Time may be the limiting factor for Starlings. Dispersal of the Starling into areas outside the northeast and east-central regions has been since 1926 (Kalmbach, 1928), and insufficient time may have lapsed for breeding populations to build up to levels similar to those in the northeast. If time is the limiting factor, both martin and sparrow populations can be expected to decrease as the Starlings become more established.

FUTURE WORK

The Purple Martin survey has been continued and enlarged since 1971 in order to monitor population fluctuations. It is pure serendipity that in 1972, after population levels had been documented for one year, Purple Martin populations were decimated by Hurricane Agnes (see Tate, 1972). Thus, with knowledge of previous levels, we can quantify the effects of the storm on martins as well as their reestablishment. Other work stemming from the survey will include multivariate analysis of the data sets presented here and

behavioral and ecological studies of nest site selection and interspecific competition. Persons interested in participating in the survey are urged to contact the senior author.

SUMMARY

A public response survey seeking information about Purple Martin, House Sparrow, and Starling populations and nest site characteristics reveals that: 1, significant geographic variation occurs in the rate of occupancy of apartment houses by Purple Martins and House Sparrows; 2, height of apartments has no significant effect on the rate of occupancy by any of the species; 3, apartments farther than 30 m from the nearest building had significantly fewer martins than closer apartments; 4, there may be fewer martins and more sparrows occupying apartments as height of vegetation increases; 5, in Mississippi, martins show a significant preference for and sparrows a significant avoidance of gourds as nest sites; 6, Starlings may avoid aluminum houses; 7, martins may prefer white apartments while Starlings may favor darker ones; 8, martins tend to prefer apartments that have not been cleaned out after a previous occupancy; 9, suburban have significantly fewer martins than do urban or rural colonies and rural tend to have fewer sparrows than do suburban or urban colonies; 10, the presence of a pond, lake or stream within sight of the apartments may result in a greater occupancy by martins; 11, the presence of other apartment houses within one-half mile has no significant effect on occupancy by martins, but may result in a greater occupancy by sparrows; 12, significantly fewer apartments are occupied the first year by martins than in subsequent years; 13, competition between martins and sparrows may result in significantly fewer martins occupying a colony, but the Starling is not a serious nest-site competitor.

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INCUBATION CONSTANCY IN THE RED-WINGED BLACKBIRD

LARRY C. HOLCOMB

Avian incubation behavior is affected by a multitude of exogenous and endogenous factors. Kendeigh (1952, 1963b) and Skutch (1962) reviewed incubation in many different orders of birds and discussed factors affecting the amount of time spent in incubation. Among workers recently reporting on incubation behavior in wild passerines are Prescott (1964), Mumford (1964), Erpino (1968), Maxwell and Putnam (1972), and Morton et al. (1972). In the Red-winged Blackbird (*Agelaius phoeniceus*), Nero (1956a, 1956b) has published observations on female behavior during the reproductive cycle, but nothing was reported on the incubation constancy (percent of daylight hours spent on the nest).

I have reported (Holcomb, 1968, 1970) that female Redwings incubated normal-sized artificial eggs a mean of 19.4 days before abandoning them. This is 8.4 days beyond the normal incubation period. The present study was designed to determine the incubation constancy in the egg-laying period, to discover if it increased each day as the incubation behavior developed, and to find if there was less incubation each day as females neared the day when eggs were abandoned in prolonged incubation.

METHODS

I studied the incubation behavior of Red-winged Blackbirds near Omaha, Nebraska, in 1968 and 1969. Birds were breeding in a variety of habitats, including weed, alfalfa, and clover fields, hedgerows, ditch banks, and marshes. I visited the nesting areas nearly every day, beginning in March and ending in August. Male Redwings generally arrived in early March and females soon afterward. Pairing began in late March and continued through April and early May. Once breeding began, I searched for nests each day, with attempts made to discover nests during nest-building and to follow them daily to termination of breeding activity.

The normal incubation period of Redwings is 11 days (Allen, 1914). To prolong incubation, I placed four artificial eggs of the same size and coloration as normal eggs in nests. These eggs were made of liquid plastic or plaster-of-paris in molds of Silastic (a commercial product). The molds were cast from Redwing eggs, and the imitation eggs were painted with water-resistant acrylic paints.

Incubation constancy was studied by two methods. The first was through watching an incubating female from a small tent, six to 10 meters from a nest. The tent was usually put in place the day before beginning observation, and females appeared generally undisturbed by the presence of the tent and observer. Time intervals for on-and-off periods were recorded to the nearest one-fourth minute, and each session of observation lasted two to three hours.

The second method of recording incubation constancy was with a battery-powered con-

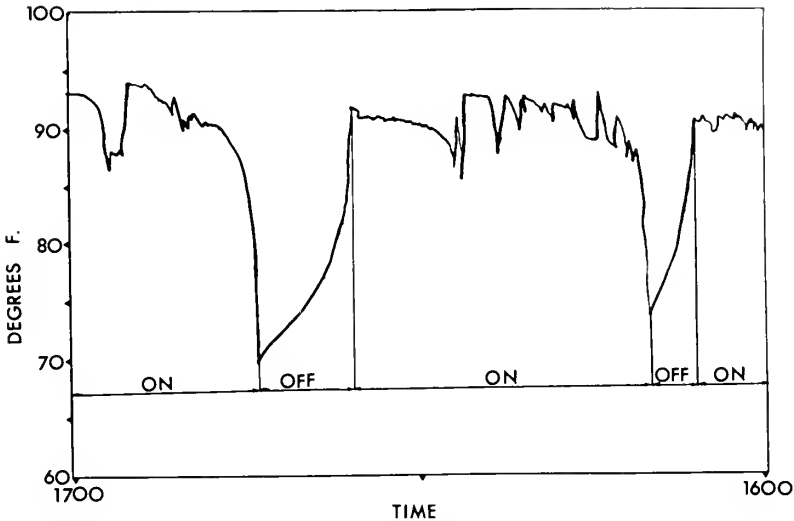


FIG. 1. A tracing of a continuous machine-recording of egg temperature ($^{\circ}\text{F}$), indicating times the female Redwing was on or off the nest. The minor oscillations on the recording occurred when the female arose to turn the eggs, preen, or shift on the nest. (Note that the tracing proceeds from right to left, as it appeared on the original recording.)

tinuous recorder. One end of a copper-constantan wire with a thermocouple was run through the bottom of a nest and embedded in a plaster of paris egg; the latter was glued securely to the bottom of the nest. The thermocouple in the egg was either flush with or not more than one-half mm below the top surface. The recorder wire was run 25 to 400 feet to a Speedomax W Recorder (117V, 60 cycles, 30 amp) that would record temperature between 20° and 120° F (-6.7 to 48.9° C).

Temperature changes caused by presence or absence of an incubating female were relayed to the recorder with an adjustment speed of one sec. These data were recorded on chart paper, and recording was continuous. Initially, recording was at the rate of one in per hr, but this was later changed to six in per hr, so that on-and-off periods could be determined to the nearest one-fourth min. In 1968, the availability of DC current permitted a few nests to be monitored and recorded 24 hrs per day. In 1969, to give greater flexibility and selectivity, a battery was used as a power source. The battery (12 volt, 100 amp hr, 88 lbs) was changed daily, and batteries were recharged each day, giving power for 13 to 17 hrs of operation each day at full charge. I used an inverter to obtain 117 volts from the battery. Care was taken to select an inverter that would run continuously and keep constant the frequency in cycles per sec and chart speed on the recorder. The unit of the recorder, inverter, and battery was set in a box for protection from weather. A sample of the continuous record of incubation behavior is shown in Figure 1, and this record constitutes the heating curve.

The continuous recorder often ran well into the night (on occasions all night), as it recorded temperature. I checked recorded temperatures and the slope of the heating curve to discover if there was a gradual development of incubation temperature and whether

TABLE 1
INCUBATION CONSTANCY IN THE EGG-LAYING, NORMAL INCUBATION, AND PROLONGED
INCUBATION PERIODS OF RED-WINGED BLACKBIRDS

| | Number of females | Total hours of daytime observation | Mean (as percentage) constancy \pm SE |
|----------------------|-------------------------|--|---|
| Egg-Laying | | | |
| Day 1 | 5 | 39.9 | 15 \pm 8 |
| Day 2 | 8 | 48.6 | 24 \pm 5 |
| Day 3 | 14 | 67.7 | 60 \pm 4 |
| Day 4 | 10 | 41.0 | 68 \pm 4 |
| Day 5 | 1 | 4.7 | 72 — |
| 2nd-to-last day | 4 | 25.9 | 35 \pm 9 |
| Next-to-last day | 9 | 57.2 | 51 \pm 8 |
| Last day | 15 | 78.1 | 65 \pm 4 |
| Normal Incubation | | | |
| Day 1-3 | 17 | 226.8 | 71 \pm 2 |
| Day 4-6 | 16 | 279.5 | 72 \pm 3 |
| Day 7-9 | 15 | 272.9 | 69 \pm 3 |
| Day 10-12 | 22 | 325.6 | 64 \pm 2 |
| Prolonged Incubation | | | |
| Day 13-15 | 25 | 411.6 | 58 \pm 3 |
| Day 16-18 | 18 | 262.6 | 59 \pm 3 |
| Day 19-21 | 9 | 104.1 | 47 \pm 7 |
| Day 22-25 | 4 | 42.6 | 32 \pm 11 |
| 3rd-to-last day | 16 | 102.3 | 58 \pm 4 |
| 2nd-to-last day | 17 | 117.4 | 56 \pm 4 |
| Next-to-last day | 19 | 153.1 | 48 \pm 4 |
| Last day | 19 | 97.8 | 38 \pm 5 |

differences might occur between a first nest of the season (when the incubation patch would be developing for the first time) and later nests (where the incubation patch might be partially developed or at least completely defeathered). If the female is capable of producing normal incubation temperatures, the slope of the heating curve should be steep; if her ability to warm the eggs is reduced, the slope should be more gradual.

Altogether, I monitored a total of 649 hrs of incubation behavior by direct observation and 1486.6 hrs by the continuous recorder. As the data were voluminous, I analyzed it by computer to determine the percent of time spent on the nest during egg-laying, normal incubation, and prolonged incubation. Statistical analysis was by means of a Student's t-test, with significance considered to be at the .05 level.

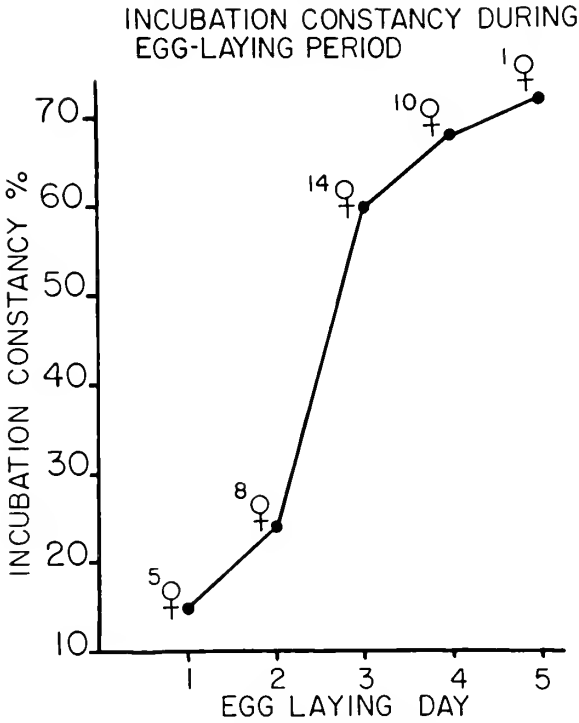


FIG. 2. Incubation constancy in Red-winged Blackbirds, demonstrating the increase from the laying of first to last egg.

RESULTS

The incubation constancy in the egg-laying, normal incubation, and prolonged incubation intervals is summarized in Table 1. Incubation begins on the first day of egg-laying, and constancy increases each day thereafter until all eggs are laid (Fig. 2). Because females lay variably-sized clutches (2-5, usually 3 or 4 eggs), incubation constancy was also calculated on the basis of second-to-last, next-to-last, and last day of egg-laying; constancy values are 35, 51, and 65 percent, respectively.

There was a significant increase in constancy from the second-to-last day of egg-laying to the last day of egg-laying. Incubation then remained high through normal incubation, with a significant decrease between days 10 to 12 and 13 to 15. It then continuously declined until birds abandoned nests.

Incubation constancy remains highest during the days of normal incubation (days one to 12). It gradually lessens during prolonged incubation, until the female abandons; days 22 to 25 show the lowest values, at 32 per-

TABLE 2

INCUBATION TEMPERATURES, ATTENTIVENESS AT NIGHT, AND SLOPE OF EGG-HEATING CURVE IN THE EGG-LAYING AND EARLY INCUBATION PERIODS IN INDIVIDUAL FEMALES

| Time of reproductive cycle | Female on at night? | Temperatures of eggs during day (°C) ¹ | Temperatures of eggs during night (°C) ¹ | Slope of heating curve ² |
|----------------------------|---------------------|---|---|-------------------------------------|
| Egg-laying | | | | |
| Day 1 | No | 30.0-32.8 | — | Steep |
| Day 1 (3rd to last) | No | 35.0-39.4 | — | Steep |
| Day 2 (2nd to last) | Yes | 35.0-39.4 | Normal | Steep |
| Day 1 (2nd to last) | No | Peak 35.6 | — | Steep |
| Day 2 (next to last) | No | Peak 33.9 | — | Steep |
| Day 2 (next to last) | Yes | 32.2-34.0 | 26.7-29.4 | Gradual |
| Day 3 (last egg) | Yes | 35.0-36.7 | 31.1-33.9 | Gradual |
| Day 3 (last egg) | Yes | Normal | Normal | Steep |
| Day 3 (last egg) | Yes | 38.3-40.0 | 36.1-37.2 | Steep |
| Incubation | | | | |
| Day 1 | — | 36.1-38.9 | 32.8-35.0 | Gradual |
| Day 1 | No | 35.0-38.3 | — | Gradual |
| Day 3-incub. | — | 36.1-38.9 | 35.6-36.7 | Steep |

¹ Normal temperatures are 35 to 40°C.² Slope of heating curve described in Methods.

cent constancy of incubation. As females usually abandon normal-sized eggs after 13 to 26 days—mean 19.4 (Holcomb, 1970), constancy values were calculated with respect to the last day before the nest was abandoned. Thus, for third-to-last, second-to-last, next-to-last, and last day of incubation, the values were 58, 56, 48, and 38 percent, respectively. There was a significant decrease in the incubation constancy between the next-to-last and last day of incubation.

No female incubated on the night after the first egg was laid (Table 2). If a clutch of three eggs were laid, a female usually incubated the night after laying the second egg; however, in one case a female did not begin incubating until laying the last egg. If four eggs were laid, a female usually did not stay on the nest at night until the third egg was laid; however, one female nesting in late May (probably her second nest) began incubating the night the second egg was laid. Another female did not incubate the night of day one of incubation. Unfortunately, there was no record available for her on the preceding night, but she incubated well on day one and continued normal incubation thereafter.

Females usually remained on the nest in the early morning until about a half-hour before sunrise. At night, they would usually get on the nest for

TABLE 3

INCUBATION TEMPERATURES, SLOPE OF EGG-HEATING CURVE, AND TIME OF DAY WHEN REDWING FEMALES ABANDONED THE NEST AFTER PROLONGED INCUBATION

| Day relative to day of egg abandonment | Temperatures of eggs on day of abandonment, ($^{\circ}\text{C}$) ¹ | Temperatures of eggs on night preceding abandonment, ($^{\circ}\text{C}$) ¹ | Slope of heating curve ² | Time of day of egg abandonment ³ |
|--|---|--|-------------------------------------|---|
| Next-to-last day | 36.7-38.9 | — | Steep | — |
| Last day | Peak 36.7 | 36.7-38.3 | Gradual | 09:40 |
| Last day | Normal | Normal | Steep | 20:53 |
| Last day | Normal | Normal | Steep | 10:05 |
| Last day | Normal | Normal | Steep | 19:05 |
| Last day | Not above 35 | Normal | Gradual | 07:00 |
| Last day | Normal | Normal | Steep | 06:45 |
| Last day | Normal | Normal | Steep | 18:30 |
| Last day | Normal | Normal | Steep | During night |

¹ Normal temperatures are 35 to 40 $^{\circ}\text{C}$.

² Slope of heating curve discussed in Methods.

³ Central Daylight Saving Time.

the last time 20 to 30 min after sundown, but occasionally they would get on and off the nest until well after dark.

Before abandoning a nest after prolonged incubation, a female remained on the nest all night previous to her last day (Table 3). Most of the time spent in incubation by females on the last day of incubation occurred in the early morning hours; about half the females abandoned in the morning and the others in the afternoon.

The slope of the recorded heating curve was very steep during the normal incubation period (Fig. 1). Table 2 shows that in the first nest of the year, peak egg temperature is not attained until at least day one of incubation and perhaps not until later. The slope of the heating curve was gradual until day three of incubation, suggesting that the development of the incubation patch may affect ability to heat eggs. Incubation patches in this species show some development during egg-laying, but peak development occurs during the incubation period (Selander and Kuich, 1963).

In females nesting for at least a second time, incubation temperatures and slope of heating curves during egg-laying compared closely to later incubation temperatures. It is not known to what extent the incubation patch changes in the interval after the first clutch is lost and laying begins in a renest. However, from these temperature data, it appears that vascularity changes very little. This carry-over would provide a greater ability to keep eggs warm earlier in the egg-laying period, compared to females on their first nests.

Table 3 shows that most females kept their eggs as warm on the last day of prolonged incubation as in normal incubation and that the slopes of the heating curves were usually steep. However, two females showed more gradual heating curves and less ability to keep eggs warm just prior to abandoning. It may be that these females were simply not in close contact with the eggs. However, in the direct observation studies of several females on the last day of prolonged incubation, they all appeared to sit as deep in the nest as observed previously.

DISCUSSION

Contrary to the general situation reported for passerines by Lehrman (1961), incubation by female Redwings begins during egg-laying, and effective incubation temperatures develops by the day that the last, if not second-to-last, egg is laid. This early development of incubation behavior and effective egg temperature result in the asynchronous hatching, which is believed to be important in the reproductive success of altricial birds (Ricklefs, 1965, 1968a, 1968b). Lack (1947, 1954, 1966) reported that in species of birds having asynchronous hatching, brood size may be adjusted to fluctuations in food availability. In times of food shortage the oldest and largest are fed at the expense of smaller and weaker nest-mates, insuring them among the offspring the best chance to survive. Observations on nestling growth (Holcomb and Twiest, 1971) show that brood reduction by starvation indeed occurs in Redwings, which may hatch up to 48 hours apart in a given nest.

After reviewing data from my other studies I suspect that asynchronous hatching exists in many passerine species; I have personally observed at least 24 hrs between the hatching of the first and last eggs in 25 species of passerines. Contrary to Lehrman (op. cit.), I believe that this asynchrony is due to some degree of effective incubation developing during the egg-laying period.

Recently, Eisner (1969) reported that captive Bengalese Finches (*Lonchura striata*) begin to incubate up to three days before the end of egg-laying. As in Redwings, the Bengalese Finch was found to incubate artificial eggs past normal hatching time. Prolonged incubation usually ended 10-15 days beyond normal incubation, compared to about eight and a half days in the Redwing. Eisner comments that this prolonged period corresponds to the length of time that the parents would be caring for chicks, had normal hatching taken place. The same relationship applies as well to the Redwing, as the young leave the nest at a mean of about 9 days.

Kendeigh (1952) has reported that House Wrens (*Troglodytes aedon*) incubate essentially uniformly throughout normal incubation, with a mean of 58.2 percent of the daylight time spent on the nest. Skutch (1962) reports

that in most species where a single parent incubates, the eggs are covered from 60 to 80 percent of the daylight time. The 65 to 72 percent recorded for the Redwing falls well into this category. The Common Grackle (*Quiscalus quiscula*) averages slightly higher than the Redwing, at 76 percent (Maxwell and Putnam, 1972). As in the Redwing, in Grackles the constancy decreased in prolonged incubation, the average being 44 percent. For Redwings, the prolonged incubation constancy ranged from 59 to a low of 32 percent.

Kendeigh (1952) reported that age of female, a change of mate, or progression of the nesting season did not seem to govern constancy in normal incubation in House Wrens. He did find a tendency toward less incubation when ambient temperatures were higher. Drent (1973) reported that egg temperature may affect the length of attentive periods, suggesting, as did Kendeigh's data, that if eggs are cooler because of ambient temperature effects, the constancy may remain higher. Although data are not presented here for the Redwing, qualitative observations show that females do show a decreased constancy as warmer ambient temperatures develop throughout the day. However, Redwing females protect eggs from direct sunlight in the hottest portion of the day.

The temperatures of incubated Redwing eggs (Tables 2 and 3) generally range higher than those (near 35.0° C) reported by Kendeigh (1963a) for the House Wren; however, he was measuring average internal egg temperatures. The interior temperatures of eggs average less than those taken at the top of the egg, adjacent to the incubation patch (and which are reported here in the Redwing). With thermocouples placed between eggs, temperatures obtained for several species ranged from 33° to 37° C (Rolnik, 1939; Koch and Steinke, 1944; Barth, 1949; Irving and Krog, 1956; Baerands, 1959; Kessler, 1960). Temperatures measured between eggs are different from either of the two methods discussed above and may be greater or smaller, depending upon proximity of the recording probe to the incubating adult.

Emlen and Miller (1969), in studying the nesting cycle in Ring-billed Gulls (*Larus delawarensis*), suggest that the pace-setting mechanisms of the cycle change from endogenous (hormonal) to exogenous (chick) regulators early in incubation. In Redwings this shift may well also occur, as nestlings are accepted even very early in incubation in the closely related Tricolored Blackbird (*Agelaius tricolor*) (Emlen, 1941). This acceptance (and presumed shift) occurs also in the American Goldfinch (*Spinus tristis*) (Holcomb, 1967), but it may not be the same in all species. For example, Breitenbach et al. (1965) found that chicks were not accepted early in incubation in Ring-

necked Pheasants (*Phasianus colchicus*), but were later when prolactin levels are higher (Breitenbach and Meyer, 1959).

It would be most interesting to discover what hormonal changes (or at least those changes in the ovary, oviduct, pituitary, and incubation patch) occur in females during prolonged incubation, as compared to their state in females involved in normal incubation or nestling care. I have noted (Holcomb, 1968), that if the nestling period is broken into two portions, there is a trend for ovaries and oviducts to be larger in the earlier portion. This would suggest a continued action of prolactin hormone, as an antigonadal agent, may extend over from the normal incubation period.

ACKNOWLEDGMENTS

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SUMMARY

Incubation constancy behavior of Red-winged Blackbirds (*Agelaius phoeniceus*) was studied in the egg-laying, normal incubation, and prolonged incubation intervals by direct observation and use of an automatic continuous recorder. Diurnal incubation begins on day one of egg-laying and the constancy increases each day, until the last day of egg-laying. Nocturnal incubation usually begins the night just preceding the day the last egg is laid. Incubation temperature and constancy indicate that in most nests, incubation is effective before the clutch is complete, especially in the last two days of egg-laying, when incubation constancy may exceed 60 percent. In the first nest of the year, effective incubation temperature is reached somewhat more slowly than in renests. Incubation constancy remains highest throughout normal incubation (64 to 71 percent) and is in the range of 60 to 80 percent reported for passerine open-nesters; it then declines as prolonged incubation continues, reaching a low of only 38 percent on the day the nest is abandoned.

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GENERAL NOTES

A shift in nesting habitat by a population of Common Eiders.—The Common Eider (*Somateria mollissima dresseri*) of the North American Atlantic coasts nests in forest, shrub, and grassland habitats (Gross, *Wilson Bull.*, 56:15-26, 1944; Choate, *J. Wild. Mgmt.*, 31:769-777, 1967; Bourget, *Auk*, 90:809-820, 1973; Reed, *Service de la Faune du Québec Bull. no. 18*, 1973). However, Paynter (*Ecology*, 32:497-507, 1951) reported that in 1947 the population of eiders nesting on Kent Island (a partially spruce- and fir-covered island in the Bay of Fundy), New Brunswick, Canada, was concentrated at the treeless southern end, at the expense of the north-end woodland. Twenty-six years later, in June 1973, I was intrigued to find that the bulk of eiders nesting on Kent Island were congregated under the trees. A brief census in areas of both forest and field (where ragweed, *Ambrosia artemisiifolia*, dominated) reinforced this impression.

I counted eider nests in 10 sample areas, five in forest and five in fields. Each of these 50 by 100 m (5,000 m²) quadrats was set out with a 100 m side running along the border between vegetation and rocky coastline and was then systematically covered. The eiders' preference for nesting under forest (\bar{x} 19.0 \pm 8.9 nests per 5,000 m²; 38.0 nests per ha) rather than within fields (\bar{x} 1.2 \pm 0.7 nests per 5,000 m²; 2.4 nests per ha) was clear-cut, despite the considerable variation among quadrats from the same habitat type. In contrast to the eiders, a census of Herring Gull (*Larus argentatus*) nests showed a marked preference for open field (\bar{x} 57.6 \pm 26.2 nests per 5,000 m²; 115.2 nests per ha) over forest (\bar{x} 13.8 \pm 6.1 nests per 5,000 m²; 27.6 nests per ha). The gull nests in the forest quadrats were concentrated along a narrow coastal strip; eider nests were farther inland under the heavy tree canopy.

Two lines of evidence suggest that pressure from gulls in open terrain caused the eider population to shift habitat between 1947 and 1973. Along the nearby coast of Maine, gull predation on eider nests decreases with increasing nesting cover for the eiders (Choate, *op. cit.*; Bourget, *op. cit.*). On the treeless Razade Islands in the Saint Lawrence estuary, an increase in Herring Gull nests (843 to 1,717), between 1938 and 1966, was accompanied by a decrease in eider nests (1,412 to 649) (Reed, *op. cit.*). Reed's explanation for the decrease in eider nests on the grassy Razades could hold for the shift of Kent Island birds to forest, i.e. "direct expulsion of eiders by aggressive territorial gulls [and/] or through reduced recruitment of eiders as a result of predation on their nests by gulls." The shift by eiders to woodland on Kent Island may not have occurred earlier, because, at least in the late 19th and early 20th centuries, the population of gulls nesting on the island was still rather low (Townsend, *Can. Field Nat.*, 37:141-144, 1923).

I thank W. H. Drury and H. L. Mendall for commenting on an earlier draft of the manuscript, and G. H. Grubb for help with field work.—THOMAS C. GRUBB, JR., *Department of Zoology, Ohio State University, Columbus, Ohio 43210. Accepted 31 May 1974.*

Collision between a vulture and an aircraft at an altitude of 37,000 feet.—On 29 November 1973, a Rüppell's Griffon (*Gyps rueppellii*) collided with a commercial aircraft at 37,000 ft over Abijan, Ivory Coast, western Africa. The altitude is that recorded by the pilot shortly after the impact, which damaged one of the aircraft's engines and caused it to be shut down. The plane landed safely at Abijan without further incident. The remains of the vulture consisted of five complete and 15 partial feathers from the

wings (secondaries, lesser, and underwing coverts), tail, neck, and breast. Sufficient details are apparent in these feathers to allow their certain identification as *G. rueppellii*, using comparative material in the U.S. National Museum of Natural History.

The previous record altitude for a bird-aircraft collision was of a Mallard (*Anas platyrhynchos*) at 21,000 ft (Manville, Wilson Bull., 75:92, 1963), based on feathers that I identified from the strike. That collision occurred between Battle Mountain and Elko, Nevada, on 9 July 1962. Other high-altitude records of birds include sightings of migrating geese at 29,000 ft, over the Himalayas (Griffin, Bird Migration, Natural History Press, Garden City, N.Y., 1964), and soaring Bearded Vultures (*Gypaetus barbatus*) at over 24,000 ft (Ali, Birds of Sikkim, Oxford University Press, London, 1962).—ROXIE C. LAYBOURNE, *National Fish and Wildlife Laboratory, Bureau of Sport Fisheries and Wildlife, National Museum of Natural History, Washington, D.C. 20560. Accepted 7 June 1974.*

American Coots feeding in association with Canvasbacks.—Commensal feeding associations between different species of waterbirds have been reported by several authors in recent years. Such associations have been described between Wilson's Phalaropes (*Steganopus tricolor*) and Northern Shovelers (*Anas clypeata*) (Siegfried and Batt, 1972), grebes (*Podiceps* spp.) and Cape Shovelers (*A. smithii*) (Siegfried, 1971), Little Grebes (*P. ruficollis*) and European Coots (*Fulica atra*) (Ashmole, Brown, and Tinbergen, 1956), Little Grebes and Northern Shovelers (King, 1963), Least Grebes (*P. dominicus*) and Mallards (*A. platyrhynchos*) (Paulson, 1969), and between several species of ducks and geese and Whistling Swans (*Cygnus columbianus*) (Sherwood, 1960; Bailey and Batt, 1974). Increased feeding rates by one of the participants in these associations have been reported for grebes (Siegfried, 1971; Paulson, 1969) and for phalaropes (Siegfried and Batt, 1972).

In Utah, Ryder (1959) described American Coots (*F. americana*) as "attending" feeding Whistling Swans in the spring. This behavior consisted of one to four coots circling around swans and picking up debris churned up by the latter's feeding activity. Coots were seen defending this food source from Redheads (*Aythya americana*). Ryder also observed coots attending Mallards, Pintails (*Anas acuta*), and Redheads in a similar manner.

During observations of waterfowl feeding activity on the Delta Marsh, Manitoba, in 1973, I observed an obvious and quite common feeding association between American Coots and Canvasbacks (*Aythya valisineria*). The association was observed at five different locations on the marsh between 25 August and 14 October.

Feeding Canvasbacks stirred up a great deal of debris with their feeding and rooting activity. One or two coots would commonly associate with single, or occasionally with two, Canvasbacks. In contrast to their normal feeding behavior, attending coots swam tightly around the diving Canvasbacks, turning and often spinning phalarope-like, plucking at the surface. At least 18 different coots and 16 Canvasbacks were observed feeding in this manner. Both adult and immature coots associated with Canvasbacks. On two occasions individual adult coots defended their feeding areas, once driving away another adult and once an immature coot.

Attending coots stayed very close to their companion Canvasbacks, always within a circle around a duck of approximately one m in diameter. On seven separate occasions, Canvasbacks even surfaced directly under the attending coot. Twice on these occasions the Canvasback threatened the coot: the latter quickly flapped away, but soon returned. On all other occasions the duck did not react at all, and the coot retreated briefly before

returning again in a few seconds. Canvasbacks generally displayed total indifference toward attending coots.

All feeding associations noted occurred over beds of sago pondweed (*Potamogeton pectinatus*), in water 30 to 70 cm deep. Close observations with a spotting scope revealed that the coots were primarily eating the slender, white rootstocks of the pondweed. Identification of this item was made possible by the frequent habit of the coots of plucking rootstocks from the water and shaking them before ingestion. Coots may also have been feeding to a lesser extent on disturbed invertebrates floating to the surface. Chironomid (ssp.) larvae were the most abundant invertebrates present.

Coots nearly doubled their feeding rates while associating with Canvasbacks. Associating coots were defined as those feeding within a one-m-diameter circle around a feeding Canvasback. Coots pecked at a mean rate of 31.9 (S.D. 3.7, range 24-48; 51 one min timings) per min while associating with Canvasbacks, versus a mean rate of 16.7 (S.D. 5.3, range 12-29—once 49; 66 one min timings) per min while feeding alone or in conspecific groups on the same area. These rates are significantly different ($P < 0.01$). Successful and unsuccessful pecks could not be distinguished in all cases, but the ratio did not seem to differ in attending and non-attending coots.

This feeding association appears to be beneficial to coots, and several observations indicate that these birds actively seek out feeding Canvasbacks. For example, a coot that had been feeding alone for some time swam directly (at least 50 m in just over one min) to join two Canvasbacks that had been loafing but began actively feeding. Other coots soon joined in.

Coots associated only with Canvasbacks, although other ducks were feeding in the same area, i.e., Mallards, Pintails, Redheads, Lesser Scaup (*Aythya affinis*), Gadwall (*Anas strepera*), American Wigeon (*A. americana*), Blue-winged Teal (*A. discors*), and Green-winged Teal (*A. crecca carolinensis*). Two American Wigeon and two Mallards were seen briefly associating with Canvasbacks in much the same way as the coots.

Support of the North American Wildlife Foundation, the Delta Waterfowl Research Station, Utah State University and the Utah Cooperative Wildlife Research Unit during these observations is gratefully acknowledged.—MICHAEL G. ANDERSON, *Delta Waterfowl Research Station, RR1, Portage la Prairie, Manitoba, Canada. Accepted 20 May 1974.*

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Recent observations of Thick-billed Parrots in Jalisco.—The Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) is listed in the Red Data Book (Survival Service Comm., Intern. Union Conserv. Nature and Natural Resources, Vol. 2, Morges, Switzerland, 1967) as "very rare and believed to be decreasing in numbers" and "giving cause for considerable anxiety." Concern that the species may be threatened with extinction has been expressed by Monson (Audubon Field Notes, 19:369, 1965). These sources cite lumbering in the species' montane pine (*Pinus* spp.) forest habitat, in the Sierra Madre Occidental of Mexico, as the principal cause of its decline in numbers. The closely related Maroon-fronted Parrot (*R. terrisi*) of northeastern Mexico is also thought to be threatened with extinction because of habitat destruction.

In view of the threatened status of *Rhynchopsitta*, it seems worthwhile to record our observations of *R. pachyrhyncha* on the two Volcanes de Colima, in southern Jalisco. Two flocks of Thick-billed Parrots, one with about 60 birds and the other about 15, were seen within 300 m of the summit of the Volcán de Fuego on 15 January 1972. The birds called loudly while flying overhead. On 6 January 1973 we observed a flock of approximately 120 parrots along the east slope of the same volcano, at about 2,000 m elevation. We were at the crest of a small peak, believed to be Cerro Alto, and the parrot flock circled near the edge of a ridge almost two km to the northeast. This behavior continued for about 15 min with considerable calling, and then the birds settled into the pines at about sunset. At 08:00 on 7 January, about 100 birds (probably many of the same individuals) were observed calling loudly and circling just above the tree-tops of Cerro Alto. Later in the morning, we saw a group of 30 flying Thick-billed Parrots, five of which landed and fed in the crowns of several small pines. These birds were observed at close range for almost one hr. Vegetationally, Cerro Alto is in the "arid pine-oak forest" zone described by Schaldach (Proc. West. Found. Vert. Zool., 1[1]:5, 1963), although the north slope of this small peak supports a denser, lusher forest approaching the "humid pine-oak forest" zone.

On 8 January, 12 parrots were seen from 14:00 to 15:00 at 2,800 m on the Volcán de Fuego. In addition, we encountered a flock of more than 100 individuals in flight on the west slope of the Volcán de Nieve, at about 2,900 m elevation. These birds were at least half a km away and high above the forest. We have no way of judging if this flock was the one we had seen the previous day. Our observations were from points on opposite sides of the volcanic massif, with a straight-line distance of roughly 12 km separating them.

Thick-billed Parrots were found on the Volcanes de Colima by E. W. Nelson, who took a female on 23 April 1892 (USNM 155.410), and by Beebe (Two bird lovers in Mexico, Houghton Mifflin Co., New York, 1905:250-251), who collected a female on 5 February 1904 (AMNH 804.998). During his considerable field work on the north slope of the Volcán de Nieve in the late 1950's, Schaldach (op. cit.) apparently never encountered the species. However, A. R. Phillips (in litt.) states, "The only time I ever saw what I took to be Thick-billed Parrots was high on the Volcán de Colima, going to roost in fair numbers (19 Dec. or 20 Dec. 1959)."

According to Ángel Lara (pers. comm.), manager of the University of Oklahoma Hacienda at El Cóbano, Colima, local residents in the volcano area occasionally see parrots along the road that ascends the north slope of the Volcán de Nieve, from Ciudad Guzmán, Jalisco. On our other visits to the volcanos in May 1972, 1973, and 1974, we did not see the species. We suspect that the parrots on the volcanos are wintering birds from the species' principal range in the Sierra Madre Occidental, although there is a possibility that they are local breeders. In Chihuahua, nesting of Thick-billed Parrots

takes place in August (Thayer, Auk, 23:223-225, 1906) and extends to October (Bergtold, Auk, 23:425-428, 1906). As yet, there are no records of the species on the Colima volcanos at that time of year.

In January 1973 we ascended the volcanos along the east slope of the Volcán de Fuego, along a road joining the valley town of Atenquique and the saddle between the two volcanic peaks. Several roads leave the saddle, and we found a newly constructed one that proceeded northward along the west side of the massif, gradually ascending the Volcán de Nieve. Workers with a bulldozer were extending the road at 3,200 m elevation. Along the entire 40 km of the road, the forest—including some magnificent stands of fir (*Abies religiosa*)—was almost entirely intact. However, a lumbering facility was in operation on the saddle, with its output of slats, shingles, and parts of wooden crates neatly stacked for drying. Because of this lumbering and the active paper mill at Atenquique, the future may be bleak for the forests on the volcanos and the parrots that depend upon them. At this time, there is still an abundance of undisturbed pine forest. Much occurs on steep and relatively unstable slopes, a fact that may retard its destruction by man. In addition, we noted several areas on the volcanos where numerous small pines have been planted, indicating that at least parts of the forests being lumbered may eventually be replaced.

We express our thanks to R. W. Dickerman and R. B. Payne for supplying information on *Rhynchopsitta* specimens, and to D. Amadon for permitting us to examine collections at the American Museum of Natural History (AMNH).—GARY D. SCHNELL, *Department of Zoology and Stovall Museum, University of Oklahoma, Norman, Oklahoma 73069*, JOHN S. WESKE, *National Fish and Wildlife Laboratory, Bureau of Sport Fisheries and Wildlife, National Museum of Natural History, Washington, D.C. 20560*, and JENNA J. HELLACK, *Department of Zoology and Stovall Museum, University of Oklahoma, Norman, Oklahoma 73060*. Accepted 3 June 1974.

Red squirrel attacks a Pileated Woodpecker.—On 26 March 1974 we observed a red squirrel (*Tamiasciurus hudsonicus*) attack a Pileated Woodpecker (*Dryocopus pileatus*) in our yard near Ithaca, New York. The woodpecker was perched near the base of a large white pine (*Pinus strobus*), when a red squirrel came down the trunk of the tree to go to a bird-feeder about 10 ft away. When the descending squirrel noticed the woodpecker, it made several aggressive feints towards the bird. The woodpecker threw its head backward, raised its crest, and slightly lifted and spread its wings in a threat display (Killham, Condor, 61:377-387, 1959). The squirrel retreated and then ran down the side of the trunk opposite the woodpecker. It went to the bird-feeder and ate seeds on the ground for several minutes. Suddenly it ran back up the tree, and then came down the trunk toward the Pileated Woodpecker, again making aggressive feints. This time the woodpecker jumped off the trunk onto the ground and gave its threat display as before. The squirrel then leaped onto the woodpecker's breast, and the two struggled briefly and silently before the bird broke away and flew high into another tree. The squirrel ran up the pine and chattered, apparently unharmed.

We can suggest no reasons for this aggression, although the proximity of the food in the unnatural setting of a feeding station may create conflict where abnormal densities and aggregations of species occur. The squirrel could easily descend the large tree without encountering the woodpecker, and neither species was near its nest. A literature search revealed no reports of similar encounters; however, Klugh (J. Mammal., 8:1-32, 1927) observed that red squirrels will chase birds from their food caches, although he

saw no attacks. Perhaps other birds tend to fly away, rather than remain in place as did the Pileated Woodpecker. Bent (U.S. Nat. Mus. Bull., 174:13-115) and Hoyt (Ecology, 38:246-256, 1957) report that Pileated Woodpeckers will feed on fruit and nuts on or near the ground, but they mention no conflicts over food. Other reported cases of interspecific aggression involving Pileated Woodpeckers have occurred when the birds were defending their nests against predators or nest-hole competitors (Bent, *ibid*; Hoyt, *ibid*; Kilham, *ibid*; Nolan, Wilson Bull., 71:381-382, 1959).

We would like to thank Peter Feinsinger and Lawrence Kilham for reviewing this note.—B. J. RATHCKE, *Department of Entomology, Cornell University, Ithaca, New York 14850* and R. W. POOLE, *Biometrics Unit, Cornell University, Ithaca, New York 14850*. (Present address of BJR: *Section of Population Biology and Genetics, Brown University, Providence, Rhode Island 02912*.) Accepted 3 June 1974.

Eastern Kingbird in Paraguay.—No specific record seems to exist of the occurrence of the Eastern Kingbird (*Tyrannus tyrannus*) in Paraguay. Hence, a specimen (DMNH 30.959) taken there on 26 October 1972 is of interest. The bird, an unsexed adult (skull ossified), was taken in the Department of Boquerón, at Teniente Ochoa (21° 42' S, 61° 02' W), at km 557 on the Trans-Chaco Highway. The senior author was the collector and the preparator Juan Guggiari. The presence of this kingbird in northwestern Paraguay is to be expected, as the species is known to range southward to southern Bolivia and northwestern Argentina (Tucumán) (de Schauensee, *The species of birds of South America and their distribution*. Livingston Publishing Co., Narbeth, Pa. 1966).—GREGORY SCHMITT, *P.O. Box 97, Kirtland, New Mexico 87417* and JOHN P. HUBBARD, *2097 Camino Lado, Santa Fe, New Mexico 87501*. Accepted 17 May 1974.

Behavioral interactions and the dispersal of the family in Black-capped Chickadees.—Most studies of the family life of young birds after they leave the nest have been descriptive, with little quantitative behavioral data. My objectives were to study how parent and young Black-capped Chickadees (*Parus atricapillus*) interact and to gain insight into the causes of dispersal. Special attention was focused on aggressive behavior.

The study took place at The University of Wisconsin-Milwaukee Field Station, Saukville, Wisconsin, from 2 June to 14 August 1972. Every adult bird had its own color band combination. Forty-four nestlings were banded using the same color band combination for all young in a family. Six families were studied.

Becoming independent and finally dispersing from the family group is a gradual process, which begins a week or so after the young leave the nest. As the young began to find food on their own, they begged less frequently from their parents (Fig. 1): also, parents at about 8-10 days after fledging began ignoring the begging of young birds that were following them.

As measures of aggression I use the Bill-up Display (Smith, Publ. Nuttall Ornithol. Club, No. 11, 1972)—a common threat display, Supplanting Call (Dixon, Stefanski and Folks, Auk, 87:322-328, 1970)—a vocalization commonly associated with attacks, and lunges at or chases of one bird by another. These aggressive acts were counted and averaged over five min periods, based on approximately 10 hr of observation for each two-day period (Fig. 2). Very little aggression was noted among family members in the first ten days after fledging, with the exception of some chasing. Aggression between members of the family increased in the latter half of the fledging period. The young became more aggressive toward each other. The parents, particularly the male, became

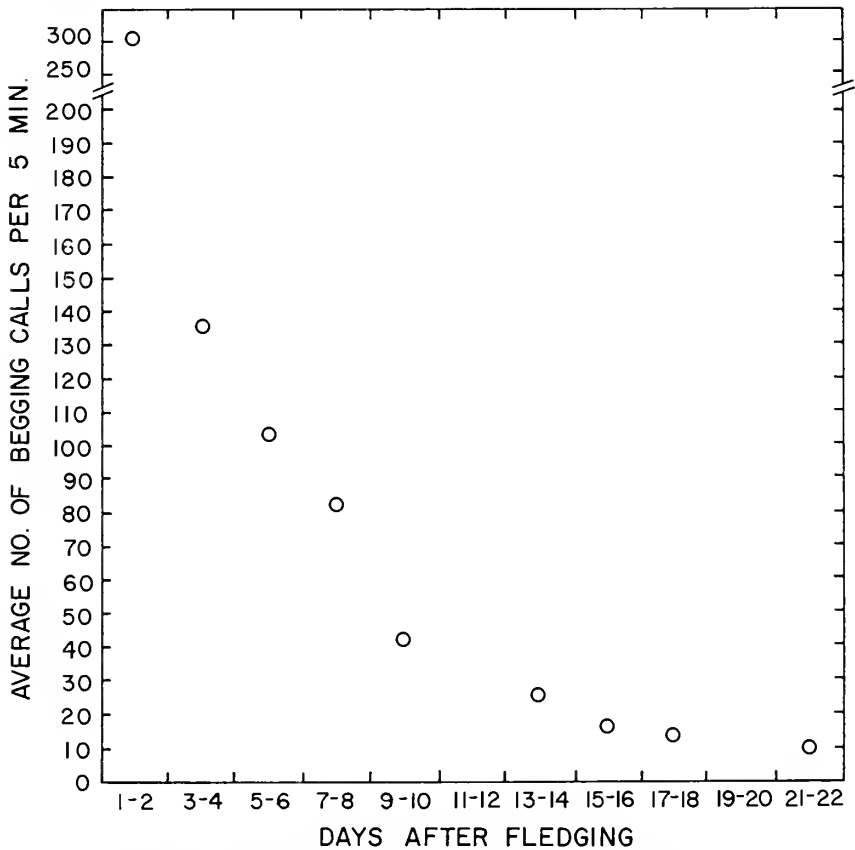


FIG. 1. Number of begging calls by young Black-capped Chickadees at various times after fledging. The observations per day were 3-6 hr.

more aggressive toward the young during the period in which the young have decreased begging and are beginning to feed independently. This change in parental behavior may be at least partially because of a change in stimulation received from the young, i.e., less begging. Begging postures in many songbirds function as submissive signals and reduce attacks. Perhaps as a result of this increasing aggressiveness, the average distance between young and their siblings and between young and their parents increased from a few ft, immediately after fledging (12 hr of observation), to as far apart as 100 ft, near the time of dispersal (30 hr of observation). Initially there are attachments among family members, as reflected in the tendency of the family to stay together. These attachments are replaced by intolerance. The final breakup of the family group is probably brought about by the increasing aggression of the parents toward the young and of the young toward each other.

Dispersal occurred about 20 days after fledging. After breakup of the family, the young became members of a group consisting of at least one adult pair (whose territory the

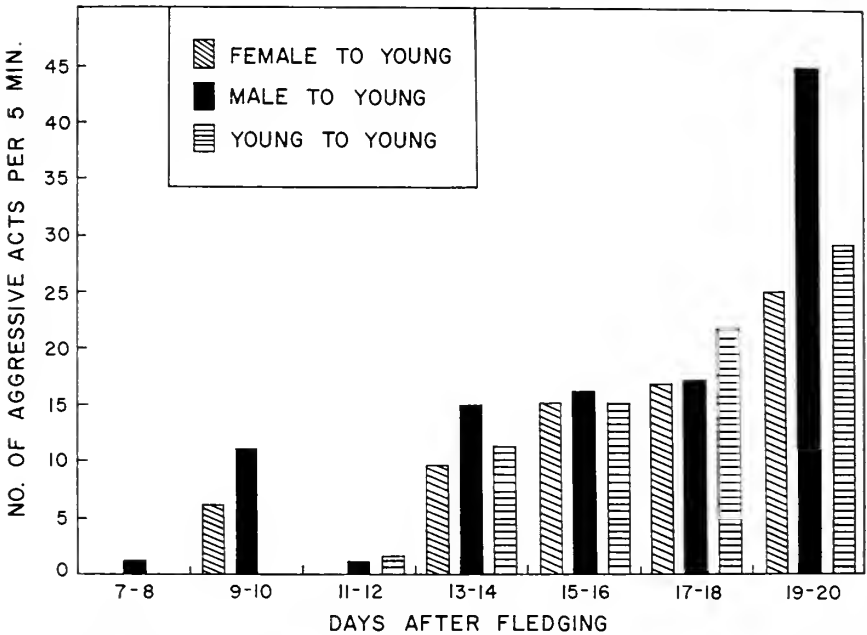


FIG. 2. Number of aggressive acts among family members of Black-capped Chickadees at various times after fledging. Observations per day were 3-6 hr.

group lives in) and young of a variety of different families. Similar flock formation has been suggested to occur in this species by Wallace (Bird-Banding, 12:49-67, 1941) and in the Carolina Chickadee (*P. carolinensis*) by Dixon (Proc. XIII Internat. Ornithol. Congress: 240-258).

I thank Dr. Millicent Ficken and Dr. Charles Weise for advice on the conduct of this study and criticisms of the manuscript. Dr. Weise and John Meyer banded the birds. This study was supported by a National Science Foundation Undergraduate Research Participation Grant. This is publication No. 9 of the University of Wisconsin-Milwaukee Field Station.—MARY HOLLEBACK, *Department of Zoology, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53211. Present address: 605A North 59th St., Wauwatosa, Wisconsin 53213. Accepted 14 June 1974.*

Is the Golden-winged Warbler a social mimic of the Black-capped Chickadee?
—The Golden-winged Warbler (*Vermivora chrysoptera*) and the Black-capped Chickadee (*Parus atricapillus*) exhibit similarities in plumage and vocalizations, and we have also found that they engage in behavioral interactions. We suggest that the similarities and interactions are, in the case of the warbler, the result of direct selection. In arriving at this conclusion, we rely in part on our studies of the two species at Lake Itasca (Clearwater Co.), Minnesota, during June and July 1968-1970 and at the University of Wisconsin-Milwaukee Field Station (Ozaukee Co.), Wisconsin, in May and August 1971-1973.

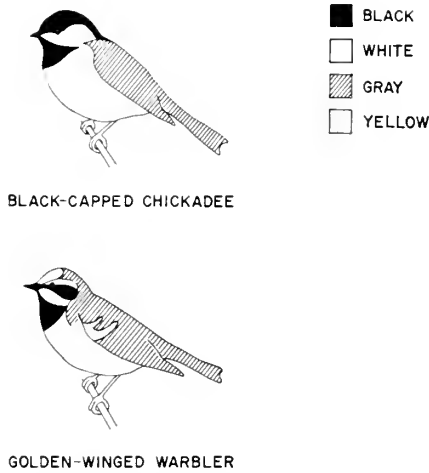


FIG. 1. Plumage patterns of the two species.

The Golden-winged Warbler resembles this chickadee in having a gray back, white breast, and black bib (Fig. 1). The chickadee has a black cap and the warbler a black face patch; the latter feature, at a distance, gives a similar impression in relation to the bib as the cap of the chickadee, i.e., a black patch separated from another by a white patch.

Although the *bee-buzz-buzz* song of the warbler and the *chick-a-dee-dee* call of the chickadee are quite different in pitch and duration, they are strikingly similar in general patterning (Fig. 2). Both frequently have a higher-pitched introductory syllable, usually followed by two to four equally spaced repetitions of a single syllable type. Despite certain dissimilarities, the vocalizations appear to have sufficient features in common to elicit interspecific responsiveness. We tested this through experiments in Minnesota, playing these vocalizations to both species along with the Ending Song (Ficken and Ficken, *Wilson Bull.*, 77:363-375, 1965) of the Chestnut-sided Warbler (*Dendroica pensylvanica*). In randomized presentations of 36 songs at 10 sec intervals, the warbler approached in response to the calls of the chickadee in nine out of 16 experiments; and in seven out of 16 experiments the chickadee approached the Golden-winged Warbler song. Neither species responded to playback of the Chestnut-sided Warbler songs. Approach responses to conspecific vocalizations were stronger than in the interspecific situation.

The Golden-winged Warbler and the chickadee have an extensive overlap in range and in habitat. The warbler inhabits shrubby fields with small trees, often with borders of taller trees. The chickadee seems to prefer somewhat taller trees, but often enters shrubbier areas to forage. The two species also have considerable territorial overlap; in Minnesota, at least 13 out of 22 Golden-winged Warbler territories were overlapped by those of chickadees.

Methods of foraging and foraging sites are also similar in the two species. In the spring the warbler obtains much of its food by probing in buds, inserting and opening its slender bill slightly to pry the new growth apart and obtain small insects. The chickadee is a

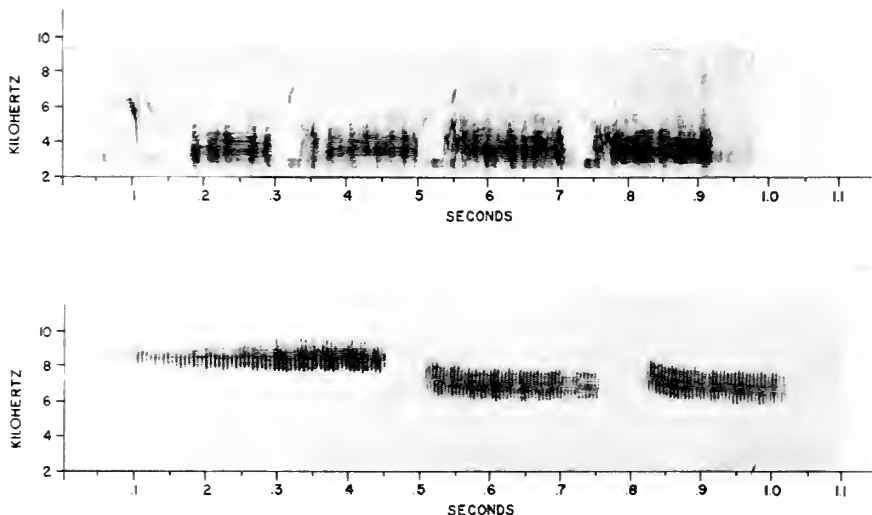


FIG. 2. Sonograms of vocalizations: top—Black-capped Chickadee call (*chick-a-dee-dee*); bottom—Golden-winged Warbler song (*bee-buzz-buzz*).

versatile feeder, but in spring it also obtains much of its food from buds. Because its bill is stubbier than that of the warbler, it cannot open buds in the manner of that species; instead it laboriously pounds them open. Both the warbler and chickadee often feed at the tips of small branches by hanging with the back downward.

During our studies, we observed Golden-winged Warblers interacting with chickadees, but not with several other small passerine species in the same habitat. An exception was behavior of Golden-winged Warblers toward Chestnut-sided Warblers; this interaction is possibly related to a releaser effect involving the yellow crowns that the species have in common. Interactions between chickadees and Golden-winged Warblers involved close approaches and following, with little aggression. This behavior was noted in fall migration and the breeding season, as well as during the spring. Either species may follow and approach the other. On one occasion during spring migration, a warbler followed a pair of chickadees (usually staying as close as 3-5 m) as they moved about 100 m through their territory. Eleven times during this association, a chickadee went directly to and inserted its bill in a bud where the warbler had been feeding. Despite a close association for at least two hr, only one aggressive interaction was noted; in all other cases when a chickadee approached a bud on which the warbler was feeding, the latter moved away. Some interactions were also observed between these species during the breeding season. On six occasions a chickadee was observed following a singing Golden-winged Warbler, as it flew from tree to tree. In addition, the use by chickadees of buds opened by warblers was also noted during the early part of the breeding season. Golden-winged Warblers also occur frequently in chickadee flocks during late summer and fall migration, although this is also true of other warbler species. Finally, although Golden-winged Warbler comprised only five percent of the arboreal warblers present during one spring migration, 50 percent of the warblers seen within five m of a chickadee were of that species.

There are several possible explanations for combinations of similarities and interaction between these two species, four of which bear mention. 1, the situation could be a case of commensalism with only the chickadee benefitting. However, if this were the case, it is difficult to explain the similarities in plumage and voice in the warbler to those of the chickadee. These features suggest that the warbler has probably converged in plumage and vocalizations, as these types of coloration and vocalization are widespread in *Parus*. 2, commensalism could be operating, with only the warbler benefitting. This would explain the convergences, but is not borne out by the behavioral interactions. 3, the similarities could be due to chance. This seems unlikely in view of the multiplicity of features and because of the behavioral interactions. 4, the warbler and chickadee may exhibit mutualism. We think that this is the best hypothesis, based on our current state of knowledge. The activities of the warbler during spring provide the clearest case. The warbler is a migrant, and the chickadee is a resident. Presumably the chickadee utilizes the best feeding areas on its territory and also might be particularly aware of predators in the area. Thus, the warbler may benefit in these two regards by seeking out the chickadees. On the other hand, the chickadee gains access to buds opened by the warbler which it would otherwise have to hammer open. We suggest that the Golden-wing may not take all the insects available from buds because the warbler is rapidly displaced by the approach of the chickadee. Interactions during the breeding season are less obvious, although the two species seem attracted to each other.

Plumage similarities between birds may result from selection for similarity in aggressive releasers related to territoriality (Cody, *Condor*, 71:223-239; Cody and Brown, *Evolution*, 24:304-310, 1970), or they may be instances of "social mimicry," involving releasers facilitating interspecific flocking (Moynihan, *Evolution*, 22:315-331, 1968). The warbler-chickadee relationship described here seems more likely a case of social mimicry, as aggression between the two is uncommon while attraction is rather frequent. The interactions of these species deserve further attention to clarify the nature of the relationship and the selection pressures acting to produce it.

We thank Dr. Jack Hailman for his criticisms of the manuscript. The study was supported by NSF grant GB 20248. Contribution No. 8 of The University of Wisconsin-Milwaukee Field Station.—MILLICENT S. FICKEN and ROBERT W. FICKEN, *Department of Zoology, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53211. Accepted 12 June 1974.*

Species-specific foraging behavior in some Hawaiian honeycreepers (*Loxops*).—Four congeneric species of Drepanididae coexist without apparent competition in the native Ohia forests of the Hawaiian island of Kauai. The species are distinguished from one another by differences in the shape of the bill and in foraging habits. In 1970-71, I had an opportunity to observe these forms in the Kokee Forest of Kauai, and I also studied in detail the exploratory behavior of three of the species in captivity. The captive specimens were raised indoors from the nestling stage by A. J. Berger and C. R. Eddinger and never foraged for food in nature. This afforded an opportunity to test whether species-specific foraging behavior was innate, or whether it was learned in the face of competition with other closely related species.

I will briefly review the feeding habits of each species as an introduction to the behavior analysis in this study. The information is from Berger (*Hawaiian Birdlife*, Univ. Press of Hawaii, Honolulu, 1973) and my own field observations. For the purpose of this paper the type of substratum used and the postures and movements of the birds are of primary interest.

Loxops virens stejnegeri is perhaps the most generalized of the species. The bill is stout, moderately long, and slightly decurved. This species feeds on nectar and on insects gleaned mainly from the surfaces of leaves and branches. It seldom ventures onto the smallest branches, the tree trunk, or the ground, and it can be characterized as a crown forager, behaviorally similar to a vireo (*Vireo*) or a white-eye (*Zosterops*).

Loxops parva is similar to *L. virens* but is slightly smaller, with the bill much smaller and straighter than in *L. virens*. *L. parva* forages in the crowns of trees and also in the underbrush. Occasionally it forages like *L. maculata* on bark and dead twigs. On one occasion I saw one fly to the ground for a moment. Its movements are quick and agile; it goes through a variety of acrobatic movements and postures, moving rapidly through a bush or tree from branch to branch or along twigs, poking curiously among leaves and flowers. This species often uses the small tips of branches, sometimes hanging upside down by one foot. The other species generally bypass these small twigs. In general movements, agility, and active nature *L. parva* is highly reminiscent of a titmouse (*Parus*).

Loxops maculata bairdi is behaviorally and ecologically rather comparable to a nuthatch (*Sitta*). Its bill is fairly long and straight. This species forages for insects on the trunks and larger limbs of trees and bushes, and it can climb head first either up or down a tree trunk and along both upper and lower surfaces of horizontal branches. This is the only one of the four species which habitually forages on the ground, a habit in which it departs from its otherwise nuthatch-like behavior. Like nuthatches, but unlike many other trunk foragers such as woodpeckers or true creepers (Certhiidae), this species does not use retrices for support on vertical surfaces.

Loxops coccinea caeruleirostris forages for insects in the crowns of trees. The tips of the upper and lower mandibles are twisted in opposite directions as in the crossbills (*Loxia*), although not to the same extent. This specialized bill is used for opening leaf buds and seed pods containing insects, in a manner similar to that by which crossbills open pine cones. Richards and Bock (Amer. Ornith. Union. Monog. no. 15, 1973) analyzed the anatomical basis for this habit in *L. c. coccinea* of the island of Hawaii. My field observations of this species were limited, and no specimens were available in captivity; consequently, the following discussion will be limited to the first three species.

In a laboratory at the University of Hawaii, captive specimens of *L. virens stejnegeri*, *L. parva*, and *L. maculata bairdi* were maintained in large flight cages. There I was able to observe them almost daily for about one year, while also engaged in anatomical studies on the Drepanididae. I soon realized that each species spent much of its time exploring and moving about the cages in a manner similar to that of foraging behavior in nature. Each cage was provided with a variety of surfaces on which the birds could move about at will: a large vertical tree trunk, with smaller branches aligned at various angles; strings hung from the screen roof of the cage; and horizontal perches. The birds were not successfully foraging for food, on these surfaces, as no insects were present. This behavior was thus presumably merely exploratory and was never reinforced by a food reward. Actual feeding was possible only from dishes along the walls of the cages, and food could be had at will.

In order to quantify my somewhat subjective impressions of these exploratory activities, I spent about six hours recording a total of 572 movements. Each time a bird changed its position, I recorded whether it was on the ground, on branches, vertically climbing, or in a hanging posture. Although all three species used virtually all postural variations, the frequency varied between species in a way which corresponds closely to the foraging behavior of the three species in nature (Table 1). As this species-specific behavior arose in captivity without experience in nature and without food reward, the conclusion is

TABLE 1
ECOLOGICAL CHARACTERISTICS AND LOCOMOTOR PREFERENCES IN THREE SPECIES
OF HAWAIIAN HONEYCREEPERS

| Species | Continental "ecological equivalent" | Main foraging substrate | No. of movements recorded | Substrate preferences in captivity (percent) | | | |
|----------------------|--|---|---------------------------------|---|----------------|---------------------------|---------------------|
| | | | | On the ground | On branches | Vertical climb- ing | Hanging postures |
| <i>Loxops virens</i> | White-eye (<i>Zosterops</i>) or <i>Vireo</i> | Medium-sized branches | 171 | | 68 | 10 | 22 |
| <i>L. parva</i> | Chickadee (<i>Parus</i>) | Small branches and twigs | 246 | 1 | 52 | 19 | 28 |
| <i>L. macalata</i> | Nuthatch (<i>Sitta</i>) | Tree trunks, large branches, and on the ground | 155 | 14 | 49 | 28 | 9 |

inescapable that it is innate or instinctive for each species. However, merely labelling a behavior pattern instinctive does not explain it. Indeed, the use of such terms, which may mask ignorance, has reached a point where some students of behavior are reluctant to use them at all. I would like to offer some brief speculations as to the nature of this "instinctive" behavior.

Innate or instinctive behavior patterns were in the past often regarded (or disregarded) as being somehow encoded into the central nervous system, where they developed during ontogeny under the control of genes. More recently, the analysis of such "instinctive" behavioral capacities as species-recognition and singing have shown that they involve specialized learning components, e.g. imprinting and the learning of species-specific songs. It is possible that some such learning activity is involved in the development of species-specific foraging behavior, such as that described above. The different species of honeycreepers probably vary slightly in their weight, limb proportions, muscle mechanics, or other factors modifying the mechanical properties of their locomotor apparatus. I do not have adequate anatomical material to examine this possibility, but I suspect that it is true in *Loxops*; it has been demonstrated in other avian groups, such as in the parulid warblers studied by Osterhaus (Amer. Midl. Nat., 68:474-486, 1962). If this is so, then certain postures and movements may be more comfortable or easily performed by one species than another. All of the *Loxops* species that I studied use all of the same postures, but in different frequencies. This means that each species is physically capable of every position, but *emphasizes* certain ones. Perhaps each individual has learned to do so by trial and error. In its early postfledging exploratory behavior an individual may find that it is more comfortable and efficient in certain postures and on certain surfaces, and hence will come to emphasize these in its foraging. In other words, the innate basis for species-specific foraging behavior may be determined more by the genes which control the development of the body and limbs than those which control the development of the brain. This would involve a simple type of learning via proprioceptive feedback from the limbs to the central nervous system. This is a simpler hypothesis than one which

postulates the existence of neural centers controlling the behavior in question, such as those postulated by proponents of theories of instinctive behavior which propose complex models of presumably inherited neural mechanisms which have no known physiological correlates in the nervous system.

This simpler hypothesis could be tested by carefully recording the movements and postures of young birds immediately after fledging and for a period of time thereafter, to see whether the species-specific locomotor pattern appears at once or only gradually.

I am grateful to Andrew J. Berger for making the birds studied available to me. This work was supported by grant no. 1-F02-GM-36, 212-01 from the National Institutes of Health.—ROBERT J. RAIKOW, *Department of Biology, University of Pittsburgh, Pittsburgh, Pennsylvania 15260. Accepted 1 July 1974.*

Foraging of Pine Warblers allopatric and sympatric to Yellow-throated Warblers.

—Pine (*Pinus* spp.) forests in the southeastern United States usually support a single nesting species of *Dendroica* warbler, the Pine Warbler (*D. pinus*). However, Ficken, Ficken, and Morse (Evolution, 22:307–314, 1968) described a case in which Pine Warblers and Yellow-throated Warblers (*D. dominica*) coexist in loblolly pine (*P. taeda*) forests on the Delmarva Peninsula of Maryland. They suggested that niche-partitioning is accomplished primarily through the ability of Yellow-throated Warblers to probe in pine cones for invertebrates, a behavior that the Pine Warbler cannot perform, because its bill is too short and its skull too large to reach to the stalk of the pine cones. In addition, Yellow-throated Warblers usually foraged somewhat higher than Pine Warblers, though overlap in this measure was high.

The present paper compares data collected upon Pine Warblers in a loblolly pine forest where no Yellow-throated Warblers occur with additional data from the Delmarva Peninsula. The primary purpose of these observations was to determine whether Pine Warblers in allopatry and sympatry forage differently. Unfortunately, I know of no pine forests occupied only by Yellow-throated Warblers, so it has not been possible to test the converse. In addition, I compare the foraging patterns of male and female Pine Warblers at both locations and relate these data to other studies.

If Yellow-throated Warblers affect the exploitation patterns of Pine Warblers, then Pine Warblers at the one-species site should forage more frequently in high positions than they do at the two-species site, for those were the parts of the habitat used most frequently by Yellow-throated Warblers. However, as the forest at the one-species site is somewhat shorter than the one at the two-species site, an absolute change in height might not occur. Further, it is possible that Pine Warblers might hawk for insects more frequently at the former location than at the latter location, as Yellow-throated Warblers in the latter hawked for insects much more frequently than did Pine Warblers.

Observations of Pine Warblers were made during March and April of 1967 and 1968 at Cedarville State Forest, Brandywine, Prince George's County, Maryland, and in March and April of 1967 at Shad Landing State Park, Worcester County, Maryland (the Delmarva site). Cedarville lies approximately 135 km WNW of Shad Landing, the study site for the two-species observations (Ficken et al., op. cit.), and is separated from it by the Chesapeake Bay. The forest at Cedarville, planted in the early 1930's, is somewhat shorter than the one at Shad Landing, averaging 15 m in height at the time of the study, approximately three m shorter than the one at Shad Landing. Other than this, the two areas are very similar, with only scattered deciduous trees and little underbrush occurring within the forest. Only a few Virginia pines (*P. virginiana*) grow on the main study area at Cedarville, although they are common in adjacent locations.

TABLE I
SECONDS SPENT FORAGING (WITH NUMBER OF OBSERVATIONS IN PARENTHESES)
BY PINE WARBLERS IN DIFFERENT STATIONS

| Height (m) | Foraging station | | | | | | | Total |
|---------------|------------------|-------------------------------|-----------------------------|--------------------|----------------|---------------------|--------------|-------|
| | Trunk | Limb, proximal one-half | Limb, distal one-half | Tips of foliage | Dead growth | Deciduous growth | | |
| CEDARVILLE | | | | | | | | |
| Male | | | | | | | | |
| 0-3 | - | 6 (1) | 186 (2) | - | 22 (1) | 12 (1) | 226 (5) | |
| 3-6 | 7 (1) | 734 (28) | 1,083 (52) | 384 (25) | 271 (13) | - | 2,479 (119) | |
| 6-9 | - | 523 (29) | 3,367 (110) | 720 (47) | 380 (13) | 133 (3) | 5,123 (202) | |
| 9-12 | - | 397 (19) | 2,020 (62) | 216 (18) | 55 (4) | - | 2,688 (103) | |
| 12-15 | - | 314 (7) | 944 (25) | 94 (3) | - | - | 1,352 (40) | |
| 15-18 | - | 8 (2) | 423 (7) | 40 (2) | 85 (1) | - | 556 (12) | |
| Total | 7 (1) | 1,982 (86) | 8,033 (258) | 1,454 (100) | 813 (32) | 145 (4) | 12,412 (481) | |
| Female | | | | | | | | |
| 0-3 | - | - | - | - | - | 27 (1) | 27 (1) | |
| 3-6 | 3 (1) | 98 (5) | 624 (16) | 53 (5) | 47 (2) | - | 825 (29) | |
| 6-9 | - | 169 (16) | 1,729 (59) | 338 (23) | 92 (8) | - | 2,364 (108) | |
| 9-12 | - | 149 (12) | 1,468 (52) | 360 (23) | 72 (2) | - | 2,049 (89) | |
| 12-15 | - | 21 (3) | 252 (8) | 97 (6) | 6 (1) | - | 376 (18) | |
| 15-18 | - | - | 5 (1) | - | - | - | 5 (1) | |
| Total | 3 (1) | 437 (36) | 4,078 (136) | 848 (57) | 217 (13) | 27 (1) | 5,646 (246) | |
| SHAD LANDING | | | | | | | | |
| Male | | | | | | | | |
| 0-3 | 14 (2) | 8 (1) | 22 (1) | 175 (17) | - | - | 219 (21) | |
| 3-6 | - | 195 (13) | 525 (28) | 423 (33) | - | 65 (2) | 1,208 (76) | |
| 6-9 | 5 (1) | 144 (9) | 995 (52) | 498 (27) | 50 (2) | 157 (2) | 1,849 (93) | |
| 9-12 | 7 (1) | 305 (17) | 1,180 (63) | 253 (19) | 63 (5) | - | 1,708 (105) | |
| 12-15 | - | 81 (8) | 886 (33) | 145 (6) | - | - | 1,112 (47) | |
| 15-18 | - | 24 (2) | 354 (16) | - | 11 (1) | - | 389 (19) | |
| Total | 26 (4) | 757 (50) | 3,962 (193) | 1,494 (102) | 124 (8) | 222 (4) | 6,585 (361) | |
| Female | | | | | | | | |
| 0-3 | - | - | 27 (1) | - | - | 170 (3) | 197 (4) | |
| 3-6 | - | 46 (6) | 275 (12) | 5 (1) | - | 97 (1) | 423 (20) | |
| 6-9 | 2 (1) | 125 (10) | 960 (39) | 229 (13) | 81 (3) | 64 (2) | 1,461 (68) | |
| 9-12 | 3 (1) | 255 (23) | 1,292 (64) | 311 (24) | 5 (1) | - | 1,866 (113) | |
| 12-15 | - | 90 (8) | 477 (25) | 145 (11) | - | - | 712 (44) | |
| 15-18 | - | - | 274 (7) | 91 (2) | - | - | 365 (9) | |
| Total | 5 (2) | 516 (47) | 3,305 (148) | 781 (51) | 86 (4) | 341 (6) | 5,034 (258) | |

Observations of feeding behavior followed those used in the earlier Shad Landing study (Ficken et al., op. cit.), with notes made of where and how each individual observed foraged for periods of up to three min following its discovery. The habitat was divided by height (into three-m segments) and part (medial and distal parts of limbs,

TABLE 2
FORAGING MOVEMENTS OF PINE WARBLERS (FREQUENCY IN OBSERVATIONS PER 1,000
SECONDS OF FORAGING IN PARENTHESES)

| Sex and locality | Seconds of foraging | Hawk for insects | Hover in foliage |
|----------------------|---------------------|------------------|------------------|
| Male, Cedarville | 12,412 | 11 (1.1) | 6 (0.5) |
| Female, Cedarville | 5,646 | 2 (0.3) | 1 (0.2) |
| Male, Shad Landing | 6,585 | 9 (0.7) | - |
| Female, Shad Landing | 5,034 | 5 (1.0) | - |

tips of vegetation, etc.) (see Table 1). Foraging motions of the birds (hawking for insects, etc.) were recorded when noted.

The Pine Warblers at Cedarville foraged somewhat lower than those at Shad Landing (Table 1); however, only in the case of females was this difference significant ($0.05 > P > 0.02$) in a two-tailed *t* test for paired comparisons (males = $0.2 > P > 0.1$ in same test). In both cases the modal height category dropped one three-m unit, which exactly matches the difference in height of the two forests.

No significant difference existed in the major positions (proximal part of limb, distal part of limb, tips of foliage) in which male Pine Warblers foraged at the two localities (Table 1) ($0.3 > P > 0.2$ in same test). A difference did occur between females at the two localities ($0.05 > P > 0.02$ in same test), with birds from Cedarville foraging somewhat more distally on vegetation than at Shad Landing.

Males did not hawk for insects with significantly different frequencies at the two localities (Table 2) ($P > 0.5$ in a two-tailed χ^2 test). Data for females were inadequate for testing, as was the case for hovering in the foliage by both sexes. No examples of cone-probing were seen.

No significant differences occurred in the locations foraged in by males and females (Table 1) (height at Cedarville, $0.1 > P > 0.05$; height at Shad Landing, $0.2 > P > 0.1$; position at both Cedarville and Shad Landing, $0.2 > P > .01$; all in two-tailed *t* tests for paired comparisons), although a trend occurred in both localities for females to forage slightly higher than males. Neither did significant differences exist in the frequencies with which males and females hawked for insects at Shad Landing (Table 2) ($P > 0.5$ in a two-tailed χ^2 test). Observations were inadequate to permit testing of other foraging movements.

The data suggest that Yellow-throated Warblers did not cause sympatric Pine Warblers to change their foraging patterns. The difference in heights frequented by Pine Warblers at the two locations can be explained as a function of the structure of the two forests. While females at Cedarville foraged more frequently in the peripheral parts of trees than their counterparts at Shad Landing, this trend runs in the opposite direction of what would be predicted if Yellow-throated Warblers were affecting their foraging patterns (see Ficken et al., *op. cit.*). As Pine Warblers at Shad Landing usually are socially dominant to Yellow-throated Warblers in encounters (Ficken et al., *op. cit.*), such a finding is not surprising. Pine Warblers prevailed over Yellow-throated Warblers in each of the 11 fights, chases, or supplanting attacks observed, this difference being highly significant ($P = 0.001$ in a two-tailed binomial test). Socially dominant species

seldom change their patterns of resource exploitation appreciably in response to socially subordinate species (Morse, in press).

Comparison of males and females suggests a pattern different from the one seen among species of *Dendroica* in spruce forests, where four or five congeners may occur. There males usually forage considerably higher than their females (Morse, *Ecology*, 49:779-784, 1968), a difference that is highly correlated with the areas in which other important activities are carried out by them (singing in the treetops by males, nesting at low to medium heights by females). While differences in the foraging heights of male and female Pine Warblers are not significant, females tended to forage slightly higher than males both at Cedarville and Shad Landing. Foraging of females centered near the height at which nests were found in the study areas (9 ± 1.0 m, $N = 5$). The low density of vegetation in pine forests relative to that of spruce forests should lower the advantage of singing in the tops of pines (vocalizations should not attenuate so rapidly) and hence the advantage to males in frequenting these areas (see Ficken and Ficken, *Living Bird*, 1:103-122, 1962). Male Pine Warblers in fact do much of their singing in the midst of foraging bouts. Males are usually socially dominant to females (12 out of 15 male-female encounters; $P = 0.036$ in a two-tailed binomial test); therefore it seems unlikely that females were excluding males from preferred locations. Smaller numbers of data upon Yellow-throated Warblers indicate that the two sexes use virtually identical foraging positions, the foraging profile for this species in Ficken et al. (op. cit.) thus serving as an accurate indicator for both sexes.

I thank M. S. Ficken, R. W. Ficken, and E. S. Morton for their comments on the manuscript. My research on warblers has been supported by the National Science Foundation.—DOUGLASS H. MORSE, *Department of Zoology, University of Maryland, College Park, Maryland 20742. Accepted 7 June 1974.*

Common Grackle kills a Barn Swallow.—During a field trip on 13 May 1973 at Joliette, Quebec, I saw a mixed flock of swallows flying over a small pond surrounded by a fence and some coniferous trees. The day was sunny and the wind light. Some Barn Swallows (*Hirundo rustica*) were resting on the ground near the water, for no apparent reason. While I was watching the swallows, a Common Grackle (*Quiscalus quiscula*), searching for food at the water edge, moved up to one of the birds and struck it on the head with its bill. The swallow gave a few wing-flaps, but died immediately. A few moments later the grackle attempted to fly away with its victim in its bill, but it dropped the swallow in the water and did not try to recover it. My examination showed the swallow had been struck just over the orbit.

Among the many reports on Common Grackles attacking small birds, the most frequent victims are House Sparrows (*Passer domesticus*), both young (Gowanlock, *Bird-Lore*, 16:187-188, 1914; Davis, *Auk*, 61:139-140, 1944; Mayfield, *Wilson Bull.*, 66:271, 1954) and adults (Hennessey, *Ottawa Naturalist*, 30:114-115, 1916; Mayfield, op. cit.; Taylor, *Auk*, 75:222-223, 1958). According to Townsend (in Bent, *U.S. Natl. Mus., Bull.* 211: 408, 1958) adult American Robins (*Turdus migratorius*) and the Gray-checked Thrush (*Catharus minimus*) are also recorded as victims. In addition, an adult Dickcissel (*Spiza americana*) (Baird and Smith, *Wilson Bull.*, 77:195, 1965), a young Cedar Waxwing (*Bombycilla cedrorum*) (Fisk, *Wilson Bull.*, 82:465, 1970), and two benumbed Pine Siskins (*Spinus pinus*) have also been recorded as killed by grackles. Finally, Christofferson (*Bird-Lore*, 29:119, 1927) reports a grackle killing a young Barn Swallow, but without saying if the latter could fly or not.

According to Baird and Smith (op. cit.), it seems improbable that the Common Grackle attacks and kills a healthy adult bird; however, a Common Grackle may attack healthy birds while they are feeding or resting on the ground. Such attacks appear to be directed only at small birds and to occur on rare occasions.—PIERRE LAPORTE, 6530 Wilderton, Apartment 30, Montreal, Quebec, Canada, H3S 2L5. Accepted 12 June 1974.

Unusual feeding habits in two species of blackbirds.—On several occasions in the period 6–10 June 1972, near Grantsburg, Pope County, Illinois, the senior author observed unusual feeding habits in a mixed flock of Red-winged Blackbirds (*Agelaius phoeniceus*) and Brewer's Blackbirds (*Euphagus cyanocephalus*). The flock, numbering approximately 300 individuals, and also including Brown-headed Cowbirds (*Molothrus ater*), was following a tractor during the disking of a 162 ha field. Many food items were unearthed as the fresh soil was exposed, and the birds were making concerted use of this prey source. As the tractor moved forward, birds from the rear of the flock would rise, fly to the front of the flock, and settle again to resume feeding. With these rear-to-front movements, the flock had an appearance similar to that described in Bent (U.S. Nat. Mus. Bull., 211, 1958), i.e. of a rolling black mass, as it followed the tractor about the field.

Mixed flocks of icterids following tractors during plowing operations are not unusual and have also been described previously (Beal, U.S. Dept. Agric. Farmers Bull., 630, 1926; Bent, op. cit.). The uniqueness of the feeding behavior reported here lies in the type of prey items taken by the two species of blackbirds. These included adult Orthoptera and Coleoptera, larval Lepidoptera, a number of forms of Arachnida, Annelida, amphibians, and mammals.

Normal food items of these blackbirds consist of both animal and vegetable matter, but the animal component is almost exclusively comprised of insects. Stomach analysis of 1,372 Red-winged and 654 Brewer's Blackbirds showed no vertebrate material in the diet (Beal, U.S. Dept. Agric. Biol. Surv. Bull., 13, 1900; Bent, op. cit.; Neff and Meanley, Wilson Bull., 69:102–105, 1957; and Soriano, Calif. Fish and Game, 17:361–395, 1931). Bendire (U.S. Nat. Mus. Spec. Bull., 3, 1895) makes brief reference to having found salamander remains in the stomachs of Redwings; however, ours apparently represents the first report of these two blackbird species feeding on frogs and mice.

The field was characterized by three distinct physiographic delineations: floodplain, sloughs, and a ridge. Most of the field was situated in floodplain, an area subject to periodic inundations by backwaters of the nearby Ohio River. Sloughs occurred throughout the floodplain, and their open waters were interspersed with dense stands of cattails (*Typha latifolia*), marsh grass (*Spartina* spp.), and other plants. The ridge area was several ft above the high water level and extended over about two to three percent of the area. A survey of the mammal populations showed the floodplain to be sparsely populated with two species of rodents: the deer mouse (*Peromyscus maniculatus*), which was distributed evenly throughout the area, and the meadow jumping mouse (*Zapus hudsonius*), which was restricted to the dense vegetation around the sloughs. The rodent density of the combined floodplain-slough area was 12.4 mammals per ha. The ridge was densely populated by prairie voles (*Microtus ochrogaster*), occurring at a density in excess of 250 per ha. This unusually high density (the density in nearby fields averaged 35 voles per ha) is thought to be the result of a recent flooding, which forced voles from the slough and floodplain areas to the refuge of the ridge. In addition to mammals, cricket frogs (*Acris crepitans*) and leopard frogs (*Rana pipiens*) inhabited the marsh grass

around the sloughs, but only young leopard frogs were observed on the floodplain away from standing water.

Blackbirds readily took and swallowed whole young leopard frogs that plowing operations disturbed in the field. The birds also pursued any adult mice that were flushed by the tractor, but both species always managed to out-distance the blackbirds, and no captures were observed. On the other hand, the blackbirds readily caught and ate nestling and juvenile voles that were present along the ridge portion of the field. As the disk would expose the voles, the blackbirds would hastily hop about, striking at the fleeing animals with their beaks. Very young voles, estimated to be from 10-14 days old and weighing up to 12 g, were easily captured and swallowed whole. Larger subadults were incapacitated by incessant pecking and then eviscerated. As adult voles were exposed, they would run distances of 3 to 5 m and then flatten themselves out on the loose soil or burrow underground. At times as many as three to four blackbirds would pursue these adults, but no captures were observed. Several times fleeing adult females had suckling young plucked from their mammae.

Following the blackbird flock and occasionally mixing with it were two to three Common Crows (*Corvus brachyrhynchos*). These were feeding mainly on the insects and annelids, as well as on the remains of the young voles that had been killed but not entirely eaten by the blackbirds. Several times the crows were observed to displace blackbirds from a freshly killed subadult vole. The cowbirds in the flock were not observed to feed on the mammals or amphibians.

Blackbird social systems, particularly that of the Redwing (Orians, *Ecol. Monogr.*, 31:285-312, 1961) are thought to have developed in response to their food resources being distributed in a patchy manner. It follows that under these circumstances, these birds would tend to be opportunistic generalists (after Schoener, *Ann. Rev. Ecol. Syst.*, 2:369-404, 1971), capitalizing on high-energy-content food when available. The facility and frequency with which both the Red-winged and Brewer's Blackbirds took the amphibians and young mammals suggest that this prey is perhaps not uncommon food, being captured and eaten whenever available.—LARRY E. BEASLEY, *Department of Zoology, University of Illinois, Urbana, Illinois 61801*, and STEVEN W. CAROTHERS, *Museum of Northern Arizona, Harold S. Colton Research Center, Flagstaff, Arizona 86001. Accepted 11 July 1974.*

Notes on birds at swarms of army ants in the highlands of Colombia.—Birds at army ant raids in the neotropical lowlands have been mentioned by numerous authors and studied extensively by Willis (*Living Bird*, 5:187, 1966; *Univ. Calif. Publ. Zool.*, 79, 1967; *Amer. Ornithol. Union Monog.*, 10, 1972). In cooler highland forests, one of the most important ants followed by birds, *Eciton burchelli*, becomes increasingly scarce, and the birds that depend upon it are seldom found above 1,000 m elevation (Willis, *Univ. Calif. Publ. Zool.*, op. cit.:6). The only other ant species commonly followed by birds, *Labidus praedator*, swarms less predictably, but it may be more important to highland birds as it ranges to higher elevations. The biology of this ant has not been studied.

As a result of the decreased importance of army ants and of ant-following birds at higher elevations, little has been reported about the highland birds that may take occasional advantage of this unpredictable food source. I have observations at seven swarms of small black ants, presumably *L. praedator*, made between elevations of 980 and 1,250 m in the Anchicaya Valley (3° 32' N, 76° 48' W), on the Pacific slope of the Western Andes, Colombia. During these observations I saw five species of birds not previously

TABLE 1
OCCURRENCE AND NUMERS OF BIRDS AT HIGHLAND ANT SWARMS IN THE ANCHICAYA
VALLEY, COLOMBIA, 1972 AND 1973¹

| Species | Number of birds per swarm | | | | | |
|----------------------------------|---------------------------------------|-------------------------------------|-------------------------------------|---------------------------------------|-------------------------------------|-------------------------------------|
| | 19 Nov 1972 (1,250 m, 13:00) | 19 Dec 1972 (980 m, 12:30) | 20 Dec 1972 (980 m, 16:30) | 14 Mar 1973 (1,050 m, 10:00) | 25 May 1973 (980 m, 16:00) | 26 May 1973 (900 m, 09:30) |
| <i>Thamnophilus unicolor</i> | 2 | | | | | |
| <i>Myrmeciza exsul</i> | | | | | | 1 |
| <i>Myrmeciza laemosticta</i> | | | | 1 | | |
| <i>Myrmeciza immaculata</i> | | 1 | 1 | 1 | 3(2 ♀) | 2(♂ ♀) |
| <i>Gymnopithys bicolor</i> | | | | | 1 | |
| <i>Scytalopus femoralis</i> | | 1 | | 1 | | |
| <i>Thryothorus spadix</i> | | 1 | 1 | | 3 | |
| <i>Microbates cinereiventris</i> | | 1 | 2 | | | |
| <i>Tangara florida</i> | | | | | 1 | |
| <i>Tangara icterocephala</i> | | | | | 10 | |
| <i>Bangsia edwardsi</i> | 2 | | | | | |
| Totals | 4 | 4 | 4 | 3 | 18 | 3 |

¹ At a swarm on 3 April 1973 (1,050 m, 12:45) I saw no birds.

known to attend ant swarms: Unicolored Antshrike (*Thamnophilus unicolor*), Rufous-vented Tapaculo (*Scytalopus femoralis*), Emerald Tanager (*Tangara florida*), Silver-throated Tanager (*Tangara icterocephala*), and Moss-backed Tanager (*Bangsia edwardsi*). The Unicolored Antshrike, a subtropical species, is to be expected at swarms, as most lowland species of antshrikes attend ant raids. All species seen at swarms are listed in Table 1.

A Rufous-vented Tapaculo was present at two swarms. Scampering among the tangle of vegetation, it foraged around the periphery of the swarm. In each case the more favorable center was occupied by an Immaculate Antbird (*Myrmeciza immaculata*). No supplanting of the tapaculo by the antbird was observed; however, a bolder Sooty-headed Wren (*Thryothorus spadix*) was vigorously supplanted twice on 19 December by a female antbird.

A large ant swarm (approximately 5.5 × 3.0 m), on 25 May 1972, was attended by three Immaculate Antbirds, three Sooty-headed Wrens, a Bicolored Antbird (*Gymnopithys bicolor*), an Emerald Tanager, and ten Silver-throated Tanagers. The tanagers moved excitedly about, 0.3-2.5 m above the swarm, as they called and foraged. Avoiding the larger antbirds, several tanagers lunged after prey, although others did not seem to watch the swarm closely for prey. My presence may have disturbed the activity of the birds, as the tanagers soon dispersed.

This is the first reported instance of any *Tangara* investigating and attending an ant-swarm, although certain lowland tanagers (*Habia* and *Eucometis*) are frequent ant-followers (Willis, Auk, 77:150, 1960). Most *Tangara* are highland birds of forest tree-tops or clearing edges; they rarely descend to the ground (I have such records only for Rufous-throated Tanager, *T. rufigula*, and Silver-throated Tanager), although they regularly feed on low fruiting shrubs of heights of 4-6 m. In the Western Andes the large

number of sympatric *Tangara* exhibit considerable specialization of insect foraging behavior (pers. obs.). As their foraging zones seldom contact ant swarms, most *Tangara* probably visit swarms only under unusual circumstances. It is of interest that the Silver-throated Tanager is somewhat less stereotyped in foraging behavior than many *Tangara* species, and it may more frequently encounter unusual food sources such as ant swarms.

On 19 November 1972, I observed another large ant raid (approximately 6.5×2.5 m) in wet, foggy forest (1,250 m) between watersheds of the Río Anchicaya and Río Verde. A pair of Uniform Antshrikes was attendant but remained slightly ahead of the swarm. Two Moss-backed Tanagers approached cautiously toward the rear of the swarm, peering intently as they watched the activity. Both birds ate berries at a nearby fruiting melastome (*Miconia majalis*) and then moved directly over the swarm, where one tanager immediately began flycatching and lunging at disturbed insects. The second tanager retired to eat a large fruit from another melastome (*Blakea podagrica*), but later it returned to the swarm and began foraging for disturbed invertebrate prey. Both birds remained at the swarm for about 12 minutes, perching 1–2 m above the swarm and at times fluttering lower (to 0.4 m) to capture prey. Neither bird descended to the ground during any prey capture or attempt.

The Moss-backed Tanager, a locally common endemic of the Pacific Andean slope, normally forages alone or in pairs among the thick mats of vegetation and epiphytes, at middle to upper levels in mossy forest. Occasionally the birds descend low to forage in fruiting shrubs, but they usually do not remain low.

These observations indicate that several highland species make occasional use of ant swarms as a food source. The importance of these ants to most highland birds is likely to be small, as the ants are not numerous and most of the birds which follow them are not professional followers.

I thank Edwin O. Willis for reading and commenting on the manuscript. John J. Wurdack identified the Melastomataceae. The Corporación Autónoma Regional del Cauca (C.V.C.), Cali, Colombia, made living in the Anchicaya Valley possible and a Peace Corps-University of Arizona program provided support.—STEVEN L. HILTY, *Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721. Accepted 8 July 1974.*

ORNITHOLOGICAL NEWS

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contribution to ornithological knowledge. Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the editor of *The Wilson Bulletin* for consideration.

Most of the statements applicable to the Fuertes Awards are also applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the colleges. High school students are eligible.

In some years two Fuertes Awards have been made, in some years, one. Amounts have been between \$200 and \$100. One Nice Award is made annually, in the amount of \$100.

Interested persons may write to Frank B. Gill, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103. Completed applications must be received by 1 April 1975. Final decisions will be made by the Council at the annual meeting of the Society, 11-14 June 1975.

FRANK M. CHAPMAN FUND

The Frank M. Chapman Memorial Fund gives grants in aid for ornithological research and also post-doctoral fellowships. Applications are due on 15 September and 15 February. Information on form and content of applications may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024.

SYMPOSIUM ON AVIAN HABITATS

The Wilson Ornithological Society and the Cooper Ornithological Society will co-host this symposium at their joint meeting at Bozeman, Montana, on 12-14 June 1975. The symposium is organized by Douglas James and will focus on birds and the vegetational environments that they occupy. John Emlen will introduce the symposium, and James Karr will present a closing summary of the papers. Speakers have already been invited, and many have already accepted and presented their titles for their papers. There will be a wide variety of subjects treated, ranging geographically from the Americas to Africa and ecologically from the tropics to tundra.

FROM THE A.O.U.

At the annual meeting of the American Ornithologists' Union in Norman, Oklahoma, on 14-18 October, the following officers were elected:

President: Donald S. Farner
First Vice-President: Charles G. Sibley
Second Vice-President: Wesley E. Lanyon
Secretary: George E. Watson
Treasurer: John A. Wiens
Editor, *The Auk*: Oliver L. Austin, Jr.

The Brewster Medal was awarded to James R. King, and the Elliott Coues Award was given to the late Robert H. MacArthur. The 1975 meeting is scheduled to be at the University of Manitoba, Winnipeg, Manitoba, Canada, on 25-29 August.

ERRATA

In Vol. 86 of *The Wilson Bulletin*, the following errors have been called to the attention of the editor:

No. 1, p. 65. The date in paragraph three should have been 1972, not 1973, in reference to the date that Olivaceous Cormorants were seen.

No. 3, p. 279. The dates in paragraphs six and seven should have been 1971, not 1968, in reference to the first dates of nesting by Brown Pelicans released in Louisiana.

At this time and with my final number, I wish to express my deep appreciation to all those who helped in publication of Vol. 86 of *The Wilson Bulletin*. In particular, I thank the scores of people who referred manuscripts and who are acknowledged here in a body rather than individually. In addition, the editorial staff is to be commended, including everyone from secretaries to the associate editors. I also express my appreciation to the authors of manuscripts submitted to *The Bulletin*, the overwhelming majority of whom endured my attempts at editing in a constructive and accommodating manner. Finally, Allen Press and its excellent staff are to be acknowledged for their continued excellent job on *The Bulletin*.—JOHN P. HUBBARD.

NOTICE TO CONTRIBUTORS

Authors are reminded that all manuscripts should now be sent to Dr. Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State, Mississippi 39762. In addition, it should be noted that Dr. Robert J. Raikow will be the Review Editor for 1975.

ORNITHOLOGICAL LITERATURE

EVOLUTION OF THE RAILS OF THE SOUTH ATLANTIC ISLANDS (AVES: RALLIDAE). By STORRS L. OLSON. Smithsonian Contributions to Zoology, No. 152, Smithsonian Institution Press, 1973:iv + 53 pp., 11 pl., 8 text figs. Paper cover. \$0.95. (Obtainable from Superintendent of Documents, U. S. Govt. Printing Office, Washington, D.C.).—Storrs Olson has spent a number of years studying rails, and this paper presents the results of his Ph.D. thesis. He summarizes and extends our knowledge about the rails of Ascension, St. Helena, Tristan da Cunha, and Gough Islands. People interested in the distribution of rails and in the evolution of flightlessness on islands will find this paper informative and necessary reading.

A new species of flightless extinct rail is described from Ascension and placed in the genus *Atlantisia*, previously containing only a rail from Inaccessible Island. Olson also adds another species to *Atlantisia*, as he synonymizes *Aphanocrex*, a monotypic genus from St. Helena. Thus, the expanded *Atlantisia* is now considered to be composed of three species of flightless rails on as many separated South Atlantic Islands. Olson believes *Atlantisia* is related to the "*Rallus* assemblage," although other than saying that there are skeletal similarities among these birds, he presents no strong evidence for this conclusion. He envisions *Atlantisia* having been derived from a single species that was given to wandering or from two closely related species. It would appear that the only recourse to these speculations is to determine the phylogenetic relationships of the recent species of rails and then fit *Atlantisia* into this scheme.

Olson also describes as new an extinct species of *Porzana*, *P. astrictocarpus*, from St. Helena. This rail was also flightless, having a greatly reduced coracoid and scapula but with a normally developed wing skeleton.

Olson takes up the problem of why some species appear to be good colonizers whereas others do not. *Porphyryula*, for example, has reached various South Atlantic islands, but it has neither colonized nor differentiated. *Gallinula*, on the other hand, has colonized and evolved flightless forms. Skeletal measurements suggest greater variability in *Gallinula*, and Olson postulates that a greater genetic plasticity has enabled *Gallinula* to adapt itself to variable environments more easily than *Porphyryula*. Olson extends this same type of argument to the Rallidae as a whole, claiming their "generalized nature" has permitted this family to successfully colonize islands. Perhaps this is so. The variability-colonizing hypothesis is an old one, and now that we are beginning to study genetic variability in natural populations through electrophoretic techniques, supportive evidence may be forthcoming.

Olson closes his paper with a discussion on the evolution of flightlessness in rails. He argues that flightlessness is an adaptation, in that a reduction of the pectoral musculature would permit a saving in energy that could be redirected to reproduction. Again, this is an old argument, perhaps reasonable—although probably not the whole story. This hypothesis is amenable to some testing, and it would be most instructive to compare the physiology and energy budgets of flightless *Gallinula* with their flying counterparts.

Perhaps the most interesting part of this paper is the discussion of how, morphogenetically, flightlessness develop. Young individuals, presumably of most species of rails, exhibit the same skeletal proportions as do the adults of flightless species. Thus, it is easy to see that if proportions of young birds were maintained through the growth process, the adults would be flightless. Various factors of the growth process might

also explain why rails more than other groups of birds frequently become flightless. In most birds that have been studied, the sternum is partially ossified at hatching or relatively soon thereafter, but in rails it apparently does not ossify until well after hatching. Much more comparative developmental data are needed, but as Olson notes, these differences in rates of ossification very possibly "preadapt" groups such as rails to flightlessness. Olson suggests that these ontogenetic changes would require little genetic modification. This may be true, but so might be the opposite speculation; I doubt whether there is evidence for either viewpoint. In any case, the degree of genetic modification does not bear on the phylogenetic usefulness of flightlessness, as he supposes. All features are of potential value in discerning monophyletic groups and cannot be rejected prior to a comparative analysis. Only after study of one or more other features that suggest alternative relationships can we say that any particular feature does or does not appear to be phylogenetically useful.

In summary, Olson has written a stimulating paper on some interesting birds and problems, and ornithologists of varying persuasions will find it worthwhile reading.—
JOEL CRACRAFT.

INTRA-ISLAND VARIATION IN THE MASCARENE WHITE-EYE *ZOSTEROPS BORBONICA*. By Frank B. Gill. Ornithological Monographs No. 12, American Ornithologists' Union, 1973:66 pp., maps, charts, drawings, photographs, color plate by W. A. Lunk. Paper cover. \$2.00 (\$1.60 to A.O.U. members). (Obtainable from Burt L. Monroe, Jr., Treasurer, A.O.U., Box 23447, Anchorage, Ky. 40223).—In 1964, Robert Storer and Frank Gill visited Reunion Island (500 miles east of Madagascar) and discovered that the endemic *Zosterops borbonica* was remarkably variable in certain plumage characteristics. They decided to recognize a record-breaking four races of the species on this single island (Storer, R. W. and F. B. Gill, *Oec. Pap. Mus. Zool. Univ. Michigan* No. 648, 1966), a bold decision in this age of lumpers. Gill returned to the island in 1967 for nine months, in order to gather detailed information on geographical distribution of the phenotypes and to answer the question—why, on an island so small (about 1000 square miles in area) is variation so great?

His conclusion contained in this monograph, was arrived at from an analysis of the plumage and size variation in relation to altitude and rainfall of 759 specimens collected at 76 localities; this is supplemented by information on courtship, feeding, movements, activity, etc. of banded birds. Gill recognized three categories of plumage variation. First were birds with gray, brown, or intermediately colored backs. As only 42 adult specimens fell into the intermediate class, and as brown and gray birds are extensively sympatric, interbreed, and produce viable offspring, this he considered an example of genetic polymorphism. Second were brown birds only, varying in head color from fully brown to fully gray, through several intermediates. Although fully brown and fully gray heads predominate, intermediates are more frequent than in the case with back color, hence this is not treated as a genetic polymorphism. Third were birds whose underpart coloration varies from nearly pure white to lead gray, with various amounts of brown in some specimens (confined to the breast and flanks). The predominance of browns and grays in the plumage, by the way, is highly unusual in the white-eye family.

What does this plumage variation mean? It turns out that there are clear and interesting geographical patterns of distribution of the phenotypes. Lowland populations are 100

percent of the brown back color morph. The proportion of brown morphs decreases gradually with altitude, and gray morphs predominate at the highest altitude. Within the brown morph, gray-headed birds are found in the wet northern and eastern lowlands (below 1380 m), while brown-headed birds are found on the dry western slopes (above 1400 m). The transition between these two types on the eastern slopes is continuous and steeply clinal, but it is abrupt in the lowlands on each side of rivers and recent lava flows. Variation of underpart color is related to altitude, as shown by regression analysis, and rainfall is additionally correlated in each of the three brown morphs but not the gray morph. In other words, some of the geographical patterns are continuous, others are discontinuous. Gill considers these patterns to indicate adaptation, possibly in relation to thermoregulation but not to predation.

The analysis of variation in wing, tarsus, and bill lengths yields a couple of surprises. Wing and tarsus lengths increase with altitude in the brown morphs but not in the gray morphs. Bill length, in contrast, bears a non-significant positive relationship to altitude in the brown-headed (brown) form, yet a significantly negative relationship to altitude exists in the gray morphs. Thus there is the interesting possibility that the two morphs respond differently to the same set of environmental factors, possibly food supply. The gray-headed brown birds show a hint of a positive relationship at low altitudes, as in the brown-headed brown birds, and a negative relationship exists at higher altitudes, as in the gray morphs. Part of these findings may be a correlated effect of body size variation, but whether we should be looking at body size, bill size, or both, the situation has greater fascination and bearing on the evolutionary history of the species than is indicated by Gill's discussion.

These are the skeletal facts of the variation, and in amassing and presenting them, Gill has done a thorough job. One may quibble with small points: coefficients of determination are woefully small; Fisher's exact test would have been more appropriate than χ^2 for the analysis of data given in Table 6; plumage might have been studied colorimetrically; multivariate statistics might have been used for unravelling the complicated co-variation of plumage and dimensions, and so on. Regardless, I doubt that the results of the descriptive study would be altered much.

In the final section, Gill attempts to reconstruct a probable evolutionary history of the species and discusses its variation, adaptation, and taxonomy. He postulates that limited primeval forest-edge habitat suitable for the species originally existed, this dissected into partially isolated patches. After the ancestral species arrived on Reunion, it lost its plumage carotenoids and the eye-ring, changes which facilitated coexistence with the aggressive and already established *Z. olivacea*. Gill supposes that *Z. borbonica* would, at that time, have resembled the present, gray *Z. b. mauritiana* on Mauritius Island (rather than being of the brown morph), because extensive phaeomelanin (brown) pigments are rare in the Zosteropidae. Next, a phaeomelanic morph may have arisen by mutation in the Reunion lowlands, where it enjoyed some unspecified selective advantage over the gray morph. There the mutant quickly spread. In response, the gray morph became better adapted to the cold temperatures and scrub vegetation of high altitudes, to which it was increasingly restricted, while the brown morph differentiated in the semi-isolated pockets of lowland habitat into the several head-color forms. The advent of man in 1663, with his subsequent habitat destruction and creation of edges, broke down the isolation. This enabled the lowland birds to increase in numbers and expand upwards and outwards, making more contacts with the gray morph. All this resulted in the pattern of distribution which is found today.

Plausible as this outline is, Gill presents it as an opinion without discussing alterna-

tives. This could have been the most interesting part of the monograph, but for me it was the most disappointing. Can it be that author or editor decided any more speculation in this section would be unwarranted?

Perhaps the original morph was brown, and it was the gray morph that arose *in situ*. Or, maybe the gray morph invaded from Mauritius, as we are told (p. 2) that "judging from the similarity of the faunas, interchange between Mauritius and Reunion islands (only 90 miles apart) must have occurred quite frequently." There may be easy ways of disposing of these possibilities, but such arguments are not given. The reader is thus left to guess why Gill chose this particular reconstruction from among the several possibilities.

In an argument that Gill could have presented, I would suggest that a monomorphic, brown-backed Reunion population was successfully invaded by a reproductively compatible, gray morph from Mauritius, which introduced genes for gray color in the head and underparts. This invasion could have happened after the beginning of habitat destruction by man, and the distribution of phenotypes and adjustments of the gray morph may not yet have reached equilibrium. This would account for the clines that exist in the dimensions of brown morphs but not the gray. The predominance of the gray-headed brown morph in the northeast may have an historical explanation, at least in part: that may be the region where the gray morph originally invaded and introduced gray-head genes into Reunion. The relationship between bill length and altitude in the gray morph may indicate that selection has operated more intensely in this dimension (for its food gathering function?) than on wing and tarsus. My invasion hypothesis would have to and could be expanded to explain why bill length decreases with altitude in the gray morph (rather than increases) and why a lowland (Mauritius) gray morph would predominate in the highlands of the much higher Reunion.

Gill's answer to the original question is disappointingly undramatic: "The highly localized differentiation of populations of *Z. borbonica* appears to have been the inevitable result of several factors, e.g., its social and sedentary habits, . . . its ties to disturbed and edge habitats, the climatic diversity of Reunion Island, and perhaps increased adaptive flexibility resulting from release from some selective agents usually present on continents, such as visual predators. In themselves each of these factors is not very unusual but they are rarely found in combination within the confines of a small oceanic island." He may be right, but even on larger islands where all these factors prevail, this degree of variation is rare. This discussion lacks depth.

Despite these few disappointments, the study is satisfyingly thorough and a welcome addition to this excellently edited and produced monograph series. Incidentally, as a result of Gill's work, the four new subspecies are reduced to the original one.—PETER R. GRANT.

EVOLUTIONARY TRENDS IN THE NEOTROPICAL OVENBIRDS AND WOODHEWERS. By Alan Feduccia. Ornithological Monographs No. 13, American Ornithologists' Union, 1973:69 pp., drawings, diagrams, photographs. Paper cover. \$2.00 (\$1.60 to A.O.U. members). (Obtainable from Burt L. Monroe, Jr., Treasurer, A.O.U., Box 23447, Anchorage, Ky. 40223.)—Fundamentalists claim that morphologists do not find missing links, that they just arrange animals like books on a shelf. I wonder how fundamentalists would react to clambering ovenbirds (Furnariidae) and scansorial woodhewers or woodcreepers (Dendrocolaptidae), groups between which there seem to be almost too many possible links.

The evolutionary relationships between these two groups are the substance of this short monograph, but despite its title, there is little on evolution within the ovenbirds. Feduccia concludes that several "intermediate" woodcreepers (*Dendrocincla*, *Deconychura*, *Sittasomus*, *Glyphorhynchus*) are anatomically so close to several ovenbirds (Philydorinae) that woodcreepers are best considered a tribe of the Furnariidae. (Technically, "Dendrocolaptidae" has priority.) Either dendrocinclas and "strong-billed" typical woodcreepers arose as separate lines from philydorines, or dendrocinclas are primitive woodcreepers that advanced little.

Combining woodcreepers with ovenbirds is not a startling idea, for there are even possible intermediates other than those Feduccia was able to study, such as *Berlepschia rikeri*. With Mayrian glasses, one can foresee that the Cotingidae-Pipridae-Tyrannidae are next. However, woodcreepers do differ from ovenbirds in pterylosis (Mary Heimerdinger Clench, pers. comm.), in having toes modified for climbing, and to a lesser extent in other characters. Intermediates do not make lumping two groups necessary, so long as there is one adaptive character that arose monophyletically in one group. Feduccia's case would be stronger if he could say that woodcreepers arose polyphyletically.

In discussing relationships, Feduccia could have used more anatomical, biochemical, and behavioral information. The hemoglobin and the anatomy of dendrocinclas may be found to have remained like those of philydorines or to have converged with them for functional reasons, e.g., the fact that neither climbs much. Contrary to Feduccia, I have observed that dendrocinclas normally do not clamber about like philydorines, but wait vertically and sally out for exposed prey or that flushed by army ants. Dendrocinclas do not flake bark or rummage, so there is little reason for them to have evolved to a strong-billed state. Lack of a pair bond may occur in *Sittasomus griseicapillus*, a fast-climbing, tiny species that pecks prey off exposed limbs in dry forests. *Deconychura longicauda* looks like a dendrocincla but climbs more; *D. strictolaema* links it to *Glyphorhynchus*.

Could dendrocinclas have arisen from leafscrapers (Sclerurinae) rather than philydorines? Leafscrapers, despite ovenbird-like slit nostrils, look and behave remarkably like dendrocinclas when clinging alarmed to the base of a tree trunk. I have found that they rarely probe mud, again in contrast to Feduccia's observation.

Could woodcreeping behavior have arisen among ant-following philydorines, as Feduccia suggests? Here he confuses the ant-following flocks, which dendrocinclas join, with the mixed wandering flocks, which philydorines join. Neither leafscrapers nor philydorines follow ants much at the present time. Perhaps earlier, before antbirds evolved so many forms, there may have been more philydorine-sclerurine intermediates low in the undergrowth, and they may have moved from searching leaf litter to letting ants do the searching. Such behavior now seems impossible. *Xenorpestes* and *Xenops* suggest remnants of an ovenbird radiation toward the understory. Modern philydorines normally forage high or intently; they do not even notice ants, unless other birds are present.

An ant-following woodcreeper could have given rise to climbing types of woodcreepers, lured to the "carrot" of food on the bare tree trunks of lowland forests and driven by the "stick" of competition from evolving antbirds. Another evolutionary route is possible, however; this could have been through small clambering ovenbirds of mixed wandering flocks (*Xenops*, etc.) to small woodcreepers like *Deconychura strictolaema*, then to strong-billed forms on one hand and through *D. longicauda* or *Sittasomus* to dendrocinclas on the other hand. Many woodcreepers follow either mixed flocks or army ants, making evolution of an ant-following woodcreeper from woodcreepers seem more likely than from ovenbirds. This would have required some convergence of dendrocinclas and

large ovenbirds. Otherwise, either clinging would have to have developed after ant-following, or the evolutionary sequence started with a very large and unwieldy trunk-climber. *Berlepschia*, however, shows that even the last suggestion is not impossible.

There are just too many possible intermediates! I wish that Feduccia and others might visit Reserva Ducke near Manaus, Brazil, where all the intermediate woodcreeper genera and several strong-billed ones—13 or more species in all—occur with a few leaf-scrapers and philydorines and nine or so species of woodpeckers. Surely guilds of trunk-climbers like these occur only in Amazonia!—EDWIN O. WILLIS.

FUNCTIONAL ANATOMY AND ADAPTIVE EVOLUTION OF THE FEEDING APPARATUS IN THE HAWAIIAN HONEYCREEPER GENUS *LOXOPS* (DREPANIDIDAE). By Lawrence P. Richards and Walter J. Bock. Ornithological Monographs No. 15. American Ornithologists' Union, 1973:x + 173 pp., 14 figs., 26 pls. Paper cover. \$6.00 (\$4.75 to A.O.U. members). (Obtainable from Burt L. Monroe, Jr., Treasurer, A.O.U., Box 23447, Anchorage, Ky. 40223).—This interesting volume has an unusual history in that it is an elaboration and refinement of the unpublished Ph.D. thesis of Lawrence P. Richards, completed in 1967. In 1968 the two authors "decided to work together on the final preparation of this study for publication, so as to bring together the special knowledge of Richards on the natural history and morphology of the Hawaiian Honeycreepers and the special knowledge of Bock on the functional morphology of the passerine jaw and tongue apparatuses." Consequently, the authors "look upon this paper as a truly cooperative undertaking in spite of the separate origins of the information and ideas used in reaching the interpretations and conclusions presented herein."

The following subjects are discussed: types of food and feeding methods, rhamphothecae of the beak, cranial osteology, jaw musculature, and the tongue apparatus. Osteology and myology are discussed in great detail, and they are illustrated by many fine drawings. The discussion of the skull of *Loxops* is undoubtedly the most complete description ever given of a passerine skull. Unfortunately, the authors use a telegraphic set of abbreviations for names, which increases greatly the task of the reader in understanding the labelled drawings. Although an appendix lists the abbreviations and full names for bones and muscles, it is much easier for the reader if complete names are included on the drawings.

Most authors have adopted the proposal of Hans Gadow that the Hawaiian Honeycreepers are related to the New World nine-primaried oscines, and specifically to the "Corebidae." Richards and Bock, however, propose tentatively to follow the suggestion first made by P. P. Sushkin in 1929 that the honeycreepers evolved from cardueline finches. Moreover, they suggest that the extinct *Ciridops anna* "may well be the closest present-day representative of the primitive stock of the Drepanididae." This differs from the interpretation reached by Dean Amadon that *Ciridops* was an advanced member of the subfamily Drepanidinae. Richards and Bock also propose that *Loxops virens* "is probably closer to the ancestral stock of the genus *Loxops* than the other known members of the genus."

There are two chief values of the monograph by Richards and Bock. The first consists of the detailed descriptions of the osteology and myology of the skull (including the tongue) and the equally detailed figures that illustrate these features. The second is the emphasis placed on the great need for thorough studies of both the anatomy and the

biology of all species of Hawaiian honeycreepers in the field before it is too late (see Wilson Bull. 84:212-222, 1972).

This reviewer was surprised at the large number of guarded and qualified statements about functional interpretations of relatively minor anatomical differences found among the four species studied and of the possible evolutionary pattern in the honeycreepers, as well as at the amount and kind of data used. For example, "an initial working hypothesis was made that muscle size is, in general, a rough index of muscle strength among homologous muscles." The authors point out (p. 14), however, that "the initial assumption used in this comparison is not valid for all comparisons of skeletal muscles as pointed out by Gans and Bock (1965). Rather one should measure the total cross-sectional area of the muscle fibers as an index to force production, the length of the fibers as an index to displacement abilities, and the angle of pinnateness as an index to the force and displacement component along the vector direction of the muscle pull. Unfortunately, these factors are more easily discussed than measured, and we realize fully the shortcomings of our comparisons in not undertaking these measurements. . . . the conclusions reached on the basis of these comparisons are relatively rough ones that do not go beyond the assumptions employed." In their comparison of the relative size of jaw muscles (pp. 74-76), the authors remark that "the muscles are ranked only in relative size with the largest muscle given the rank of '1': no quantitative values are assigned to the differences in any of these rankings. Larger muscles are assumed to be stronger, i.e., develop a greater maximum force. The only valid comparisons that can be made in these tables are horizontal ones within the homologous muscle or possibly within a set of muscles in the several taxa. Comparisons *must not* be made vertically along the columns between different muscles or different sets of muscles because the same rank, e.g., 1, in several different muscles does not imply equal size or force development."

Similarly, the attempted correlation of feeding habits with jaw morphology is based on minimal data. For the Hawaii Creeper (*Loxops maculata mana*), for example, we find (p. 21) that "out of twenty-five descriptions in my field notes twelve of these probings were at the bark of branches and trunks, seven were into hair-like lichens, two onto exposed twigs, two into moss on branches, one in rotten wood, and one underneath a flat lichen growing on a branch." Feeding habits of the Maui Creeper (*L. m. newtoni*) were observed in the field on only two days; this is one of the more common species in the Maui rain forests. Such limited observations of feeding behavior are surely inadequate for postulating elaborate analyses of bone and muscle mechanics and the possible evolutionary sequence within the genus.

Richards and Bock are well aware of the weaknesses in their presentation. In writing of the Hawaii Akepa (*Loxops c. coccinea*), they state (p. 23): "These crude data may aid in giving an idea of the food niche of this race." Of the functional interpretation of the horny covering of the bill (p. 30), they remark that "these correlations between the ramphothecal morphology and feeding observations are largely hypotheses to be tested by further observations, not proven facts." "All conclusions reached in this phase of the study [jaw musculature] are speculations and must be treated as hypotheses to be tested, not as demonstrated facts" (p. 53). In the functional interpretation of the skeletal and muscular mechanism of the jaws (p. 78): "We are clearly cognizant of the lack of essential information on the exact movements of the jaws during feeding, on the exact forces, musculature and otherwise, acting on the jaw apparatus, on the exact food preferences of each species and other equally important factors, so that these conclusions are offered only as hypotheses for further consideration and testing. In spite of their inadequate basis, these conclusions form a valuable basis for further study and we offer

them without apology." In their discussion of the correlation between feeding habits and skull morphology, they write (p. 111): "The disjointed nature of these summaries does not provide a sufficient basis for understanding the entire feeding apparatus for the feeding habits in each species of *Loxops*, and most importantly, for comprehending the adaptive history of the genus *Loxops*. The latter is essential for any future analysis of the evolution and classification of the Drepanididae, including its origin from some mainland group within the New World nine-primaried oscines." Similar qualifying statements are made on pp. 32, 84, 110, and 120.

In view of these apologetic statements, one cannot but question the justification for devoting so many pages to hypotheses, when the authors themselves acknowledge that the data are inadequate. It is important, therefore, that ornithologists study this work carefully, so that its hypotheses do not become stated facts in subsequent literature. A number of striking typographical errors are annoying.

I would point out that Richards and Paul H. Baldwin were "modern pioneers" in the study of the endemic Hawaiian forest birds. Their field work in the early 1950's ended a period of nearly 40 years during which virtually nothing was learned about the forest birds. Only someone who has worked in the Hawaiian rain forests can fully appreciate the difficulties faced by these men. I agree fully with the following statement (p. 128) made by Richards and Bock: "Hopefully the most significant result of this study of the adaptation in the feeding apparatus of *Loxops* is to provide a stimulus for additional studies on the comparative biology and evolution of the Hawaiian honeycreepers and the eventual understanding of the classical example of adaptive radiation they provide."—ANDREW J. BERGER.

DER ZUG EUROPÄISCHER SINGVÖGEL. EIN ATLAS DER WIEDERFUNDE BERINGTER VÖGEL. Part 1. By Gerhardt Zink. Vogelwarte Radolfzell am Max-Planck-Institut für Verhaltensphysiologie, Germany, 1973: loose leaf folio of 123 pp., including text, 4 figs., and 87 maps. Paper cover. DM 48.00. (Obtainable from Vogelwarte Radolfzell, D 7761 Schloss Möggingen, Germany.)—This first of three parts of an atlas on European passerine migrations contains banding and recovery data for 3,969 individuals of 30 species of the Turdidae and Sylviidae. The following species groups are included: wheatears (*Oenanthe*), chats (*Saxicola*), nightingales (*Luscinia*), grasshopper warblers (*Locustella*), reed warblers (*Acrocephalus*), Icterine and Melodious Warblers (*Hippolais*), bush warblers (*Sylvia*), leaf warblers (*Phylloscopus*), and the kinglets (*Regulus*).

About 100 passerine species will be covered when the third part of the atlas is completed. Dr. Zink, of the Vogelwarte Radolfzell, has compiled and edited this magnificent tome, resulting from European endeavors in bird-banding. It reflects enormous progress since the publication of the first such atlas by Schüz and Weigold in 1931, when all they had to rely upon where the recoveries of 27 banded birds. No ornithologist interested in bird migration and its analysis can afford to overlook this important new piece of work, but he must be cautioned, too.

The system of the atlas is plain cartography, the plotting of the banding and recovery sites of individual migrants. The author restricted his choice of species to those for which the banding and recovery data of individual birds could be plotted and read in book-size maps. An additional 25 species are mentioned only by lists of references in

small print. This is quite unsatisfactory, because it is from these latter species, such as the Barn Swallow (*Hirundo rustica*), that the banding stations have accumulated the largest samples of recovery data. These species have been disregarded simply because they no longer fit into the maps in the form of individual plottings. It is my opinion that they should have been used and analyzed in the first place as populational samples adequate for analyses with modern statistical methods. They could have yielded a new and much-needed understanding of the natural migration patterns of species, subspecies, and geographic populations.

The weakness of the atlas itself lies in its cartography. The maps are not equidistant projections and do not show equal areas. The corresponding banding and recovery sites are connected by straight lines, which are not compass directions, great circle routes (which might be a good way to characterize the migratory pathways of many migrant species), or the actual flight paths of the birds on record. Nevertheless, the plots can be determined, with some inaccuracy, by using the scale and grid markings along the edges of the maps.

According to the author's plan, the atlas contains the data for only those birds that were recovered more than 100 km from their banding sites. Samples of short-distance recoveries, although mostly large and very informative, have been altogether excluded. They should have been used, for they provide a precise and biologically meaningful determination of the flight routes and their correlations with time, space, and other environmental factors. The grid presented by the long-distance recoveries is much too coarse to provide a means for extracting such desirable information from the atlas. Information on the total numbers of birds banded or the percentages of birds recovered is lacking. Birds banded as nestlings (places of their origin) and at other times of the annual cycle are distinguished by various cartographic symbols. Unusual migratory phenomena are shown in supplementary maps, e.g., Wheatears (*Oenanthe oenanthe*) banded and recovered in Iceland. This being an atlas, the texts accompanying the maps are very brief and are limited to notations on the relevant periods of the annual cycle (migrations, winter quarters), as well as references to the material used and pertinent literature. Zink presents few of the biological and ecological data that would interest banders and that are the spice of any research in banding and bird migration. His lists of literature on the migrations of the species treated are not complete.

What, then, is the value of this atlas, apart from its meticulous documentation of a very successful part of the European bird-banding programs? It is a stimulating guide and a tool for field ornithologists devoted to banding birds. It shows clearly that the migratory patterns of the majority of the migrant species are still not sufficiently known. Through its results and weaknesses, the atlas reveals needs for certain banding projects and research on migration under natural conditions aimed at a better understanding of bird migration.

Bird-banding stations, with their vast accumulations of data steadily increasing under the enthusiastic endeavors of dedicated field ornithologists, are storehouses of a wealth of scientific information. It is a great task, and a time-consuming one, to make this dormant information available to science. This atlas has accomplished one step in this direction, but the challenge remains for the development of specific and cooperative banding programs and an efficient analysis of the banding and recovery data. Neither modern biostatistical methods nor the biology and ecology of the migrant species can be ignored in the analysis of the ever-fascinating topic of bird migration.—E. G. FRANZ SAUER.

FINCHES. By Ian Newton. Taplinger Publishing Co., New York, 1973:288 pp., charts, maps, drawings, photos. \$12.50.—North American readers may feel that this title is misleading, for the book itself is concerned almost entirely with the European fringillines and carduelines. It is, however, much more than an account of 18 European seed-eaters. As the behavior and ecology of several of the species are rather well-known, and as the birds are related species with geographical ranges that largely overlap, the author is able to provide a comparative treatment that exemplifies many basic biological problems. The book is thus to be recommended as an introduction to current problems in field ornithology, as well as for the data on the birds themselves.

The first three chapters are devoted to introducing the species. Ten of the remaining thirteen chapters are comparative, dealing with a variety of aspects of distribution, ecology, and behavior. In each of these, evidence is drawn from many of the species, and interspecific comparisons are used to give depth to the discussion. The author worked for many years with the late David Lack in the Edward Grey Institute at Oxford, and this experience must have been in part responsible for his ability to weave into coherent patterns material on breeding seasons, clutch size, aspects of ecology, and migration. The comparative material on feeding behavior, based largely on Newton's own work, is also of special interest. The descriptions of courtship behavior are necessarily condensed, but Newton's comparative approach enables him to convey a great deal of information in the space allowed.

The other chapters are concerned with what might be described as "special studies." One of these, on the breeding behavior of the Chaffinch, is largely distilled from Peter Marler's monograph on this species. The two others are both based on studies by Newton himself—one on the important economic problem which Bullfinches pose to fruit growers and the other on the movements of crossbills.

Indeed it is perhaps the author's own involvement in so much important research on finches that gives the book its special quality. The discussions are based on a detailed search of the literature (and there is a considerable bibliography), but this is tempered by the freshness which can come only with first-hand material. On top of this, Newton is a level-headed scientist, interpreting the field data in terms of evolutionary theory.

There are good color plates of the species, though the colors of some are not quite true; 24 excellent black-and-white plates, and 64 text figures. Only the tables have been printed in a somewhat less pleasing way than they could have been.—ROBERT A. HINDE.

AN EYE FOR A BIRD: THE AUTOBIOGRAPHY OF A BIRD PHOTOGRAPHER. By Eric Hosking, with Frank Lane. Paul S. Eriksson, Inc., New York, 1973:xviii + 302 pp., 16 color pls. and 124 black-and-white photos. \$10.00.—The headmaster who told his fifteen year old student, "Hosking, you'll never make anything of your life," would have been a failure as a fortune teller. For today the Cockney, Eric Hosking, is unquestionably the most noted and respected bird photographer in the world. His autobiography is an intriguing distillation of the abundant life this man has led while filming birds and other wildlife on every continent except the Antipodes. Hosking has co-authored a dozen books, furnished illustrations for 700 more, and maintained a grueling lecture schedule for thirty-two years. In his time he has become warm friends with such notables as Lord Allenbroke, Prince Philip, and Roger Tory Peterson.

The book's title is most appropriate, for Hosking lost an eye while attempting to film a Tawny Owl in 1937. A measure of this man's courage and compassion was the fact that two days after leaving the hospital he was back filming the owls and pleading with a gamekeeper not to shoot them!

An Eye for a Bird contains delightful morsels of interest to almost everyone, including historians, romantics, and women's libbers. Hosking tells us that Kites and Ravens served as the "dustmen," or garbage collectors, of London in the 17th century; that Princess Margaret, who later married a photographer, once labeled Hosking, who was on assignment at a haying party, as "a beastly old photographer"; and that a Bedouin assured him that a girl child counted as only half a person.

But it will be ornithologists and wildlife photographers who will derive the greatest pleasure from this volume, because it recounts numerous incidents that divulge hard facts about the avian world. It was Hosking's observations that established that the hen Marsh Harrier passes food to the male and that the species is polygamous. During the London blitz, he noticed that Starlings learned to imitate with frightening reality the whistling of falling bombs. Another discovery was that Ravens can count to at least four or five; in order to film the activity at a Raven's nest Hosking simply had a classroom of children escort him into his blind to deceive his subjects.

Hosking vividly describes the joys that a bird photographer may have while confined in a blind. While in a Hungarian marsh, for example, "A young moorhen came and fed just in front of my hide, a queer little thing with black body and bright red bill. Water rails belched all round, little crakes 'craked,' bearded tits pinged, Savi's warblers reeled, bitterns boomed and there was a procession of purple and gray herons flying by all the time. A dragonfly used the alley-way between the hide and the nest to fly backwards and forwards as though it was on guard duty."

Hosking's wife, who often worked closely with him, once wrote in her diary, "What a great element of chance there is in bird photography." This statement came after the Hoskings had examined—at great cost in time and energy—many Golden Eagle eyries and found none suitable for filming. Yet, wittingly or unwittingly Hosking offers a great deal of encouragement to wildlife photographers everywhere. For one thing, he proved that one does not have to specialize in exotic subjects in far-away lands to be successful in the profession. Indeed, for years he made his living from the subjects found in civilized England alone, and his most famous photograph (reproduced at least 1000 times) is of a Barn Owl, a common enough predator in more than a score of countries.

If, as Mrs. Hosking implied, luck does play a part in obtaining high quality wildlife pictures, especially those of birds, then Eric Hosking was born under a galaxy of lucky stars. This is evidenced by the dozens of superb black-and-white and color pictures scattered throughout the text.

This reviewer protests Mr. Hosking's claim that he initiated the use of pylons for bird photography in 1936. Dr. Francis Hobart Herrick built some tremendous towers of both wood and metal in order to photograph nesting Bald Eagles along the south shores of Lake Erie, as early as the 1920s.

From personal experience this reviewer suggests that when filming nesting owls it is possible to have the beam of a flashlight or even more powerful illumination on the scene at night, without causing a lessening of parental care of the young. Hosking writes of trying to trip his camera in darkness, just hoping the owls would be in the frame when the flashbulb fired.

Hosking conducted lengthy experiments with birds' defenses of their territory, and

his final paragraph on the subject might give us all pause. "In one way or another our experiments showed that a vital problem of the bird world finds its counterpart with man. A bird is at its fiercest when it thinks its living space is threatened. Is it too much to hope that man might learn something from this?"—KARL H. MASLOWSKI.

AMERICAN BIRDS. By Roland C. Clement. "Knowledge Through Color" series, no. 39. Bantam Books, New York, 1973: 159 pp., illus. Paper cover. \$1.45.—Is any other field of natural history literature so plagued with pot-boilers as is that of bird books? Week after week we see the publication of poorly-conceived, hastily assembled products, whose sole justification for existence is somebody's hope for a fast buck. Publishers are experienced businessmen, who do not package a product without a reasonable assurance that there is a market for that product. If this is so, then we must reluctantly admit that *anything* about birds will sell, judging from what the publishers offer.

A recent case in point is this Bantam paperhack. It is one of a series characterized as a "unique home reference library . . . perfect as source material for student papers . . . packed with hundreds of specially created *full-color* illustrations." All the photographs in this book are from the files of the National Audubon Society, and the text is by Roland Clement, vice president of the Society and a distinguished conservationist. The Society and Dr. Clement should be ashamed of themselves. All too many of the illustrations were "specially created" all right—by shoving captive birds into a staged background (viz. Bohwhite), by photographing cagebirds without bothering to conceal the cage (viz. American Goldfinch), or even by posing "stuffed" birds (viz. Ring-necked Pheasant). I noted only one misidentification (one too many): the female Wood Duck is actually a Mandarin Duck. Color reproduction is not bad for a cheap, mass-produced book, but a pink-billed, pink-footed Bald Eagle is a bit startling. I was not surprised when I found that all of the photographs about which I had any suspicions were taken by people I had never heard of, rather than by such naturalist-photographers as Roger Peterson, Sewall Pettingill, the Cruickshanks, or Karl Maslowski, all of whom are represented by the fine photographs of wild birds that we would expect of them.

Only 120 species are figured. Choices thus had to be arbitrary to some extent, but are sometimes oddly balanced; the three Gruiformes shown are the American Coot and *both* American species of eranes. One might have expected that selection might have leaned a little more toward species of which *good* color photographs are available. The prestige of the National Audubon Society among the American public is such that the Society does itself a disservice, in my opinion, by maintaining such low standards in its photographic files (much less allowing these to be published and credited to the Society).

The text consists of about 13 pages of highly generalized introduction to birds and bird watching, illustrated by a crude diagrammatic map of five principal "Life Zones" (not Merriam's) of North America, and a set of nine ghastly drawings of "adaptations" (3 of bill, 2 of wing, 1 of tail, and 3 of foot). Each species is given a short paragraph, with an additional paragraph introducing each order. Although some western species are figured, there is a distinct eastern bias, especially in the text paragraphs (which often mention non-figured species). Thus the only chickadee shown is the Black-capped, and half of its text paragraph is devoted to the Carolina, but no western species is mentioned. Even in these brief paragraphs, errors or gross oversimplifications occur. In the last two

dozen or so species accounts in the book I found such items as the attribution of sexual dimorphism to the Lark Sparrow; designation of a call of the Evening Grosbeak as its "song"; characters to distinguish the Bobolink in fall from "other large sparrows"; the statement that the House Sparrow is not really a sparrow but an "African Weaver"; and attribution of the word *mariposa* as the *sole* "Latin American (!) name for the whole tribe of warblers." I hate to think of any student using this book as "source material" for a paper.

A critical review of a paperback may seem like overkill, but this book can serve as an example of the mediocrities being foisted on the birdbook-buying public by hungry publishers. At \$1.45 it is not much of a bargain, which is a pity; its defects (except for color reproduction) are not a function of its cheapness, but of carelessness, undoubtedly haste, and an unconcern for the high standards we should expect from the author and the sponsoring organization.—KENNETH C. PARKES.

IN THE SHADOW OF THE FALCON. By Ewan Clarkson. E. P. Dutton & Co., Inc., New York, 1973: 186 pp., 7 drawings by David Stone. \$6.95.—The Peregrine Falcon is one of the noblest, swiftest, and most romantic birds in the world. It has been the favorite hunting bird of falconers for thousands of years. Its world-wide population had remained stable until recently, when its numbers declined at an unprecedented rate. This decline coincided with widespread use of chlorinated hydrocarbons such as DDT.

"In the Shadow of the Falcon" is the story of a pair of Peregrines and their offspring. The book begins at the cliffside eyrie off the coast of Wales and goes through an entire life cycle. Clarkson's vivid, evocative prose portrays accurately, but without sentimentality, occurrences in the life of the Peregrine Falcon. One gains the insight of what it must be like to be a falcon. Clarkson must have studied both wild and trained Peregrines for many years, in order to be able to describe so accurately the behavior and feelings of these birds. I myself have been associated closely with Peregrines for over 30 years (wild, falconry, and captive breeding) and find that the author's insight and subtle innuendoes most truly give the correct feeling of "Peregrine."

In one incident, a Black-backed Gull was about to knock a young falcon off the nest ledge. "At a moment Frika [adult male falcon] hit him, and the force of the blow pinned him to the ledge, splintering one wing and tearing a great flap of skin from his neck. Larus tore himself free and launched himself into space, one wing frantically fanning the air as he spiraled down to the waves. Freya [adult female falcon] came up from below, hit him hard, and swooped past, turning to drop and hit him again. Larus was already dead, his head half-severed from his body."

A feeling of how young peregrines learn to hunt is well portrayed in the following sentences: "Chek [the young male falcon] killed several times in the days that followed, always in company with his parents. On two occasions the prey had already been hit and wounded before he made his strike, but whether this was by accident or design on the part of the older birds may never be known. The peregrines may have been teaching Chek how to hunt, or they may simply have come to regard him as a member of the team."

An insight into the humidity requirements of developing eggs is given in the following paragraph: "Refreshed and invigorated, she would then return to the eyrie, frequently with her underskirts still damp from her bath. This did no harm, and indeed

the eggs benefited from the moisture and steamy warmth. It helped prevent fluid loss from the egg and preserved the elasticity of the shell."

There are a few slight errors in the book. In chapter 3, Clarkson writes, "The next morning there was another, and on the following day a third [egg], slightly smaller than the others." Peregrines generally lay their eggs at 48, not 24 hour intervals. Later, he states that the tiercel (male) hatched from the smaller egg, the implication being that males—which are one-third smaller than the females when fully grown—develop in smaller eggs. There is no scientific evidence to corroborate this. The following quote (p. 77) may give readers a slight misconception of the Peregrine's digestive system: "the indigestible remains of bone and feather which their crops could not digest and which they threw up after each feed." The food actually goes from the crop to the stomach, where the digestion takes place. There are no digestive glands in the crop. Hawks and falcons are able to digest bones, and rarely is there even a small piece of bone in a hawk's pellet. This is quite different from owls, which do not have crops and cannot digest bones. Their pellets usually contain all the bones and skulls of their prey. In the diurnal birds of prey (Falconiformes) pellets are not regurgitated after each "feed." The material is accumulated, and when enough is in the stomach, regurgitation occurs—normally early in the morning, as no feeding has taken place during the night. In spite of these few faults, "In the Shadow of the Falcon" has echoes of meaning for all who are concerned about the future of the earth. At the same time it is an engrossing story that will remain long in the reader's memory.—HEINZ MENG.

INDEX TO VOLUME 86, 1974

BY DAVID M. NILES

This index includes in addition to the names of genera, species, and authors, references to the following topics: abnormalities, aggression, anatomy, banding, behavior, brood size, care of young, clutch size, communication, conservation, courtship, density, display, distribution, ecology, eggs, food and food habits, growth and development, habitat, hatching, incubation, locomotion, measurements, metabolism, migration, molts and plumages, morphology, mortality, nest building, nest sites, nesting, nesting failure, nesting success, nests, parasitism, pesticides, physiology, populations, predation, roosting, taxonomy, territory, voice and vocalizations, weather, and weights. Also included are references of biological significance to reptiles and mammals. Forms described as new in this volume are given in **boldface**.

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