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THE WILSON ORNITHOLOGICAL SOCIETY

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Beechey Jays captured for flagging. Top: yearling (yellow bill, brown iris). Bottom: adult (black bill, yellow iris). Note prominent erectile crest on adult.

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SOCIAL BEHAVIOR, HABITAT, AND FOOD OF THE BEECHEY JAY

RALPH J. RAITT AND JOHN WILLIAM HARDY

As part of a long-term comparative investigation of the ecology and evolution of social behavior in the black-and-blue jays (genus *Cyanocorax*, subgenus *Cissilopha*) of Middle America we began a field study of the Beechey or Purplish-backed Jay (*C. beecheii*) in 1974. Other members of the group, particularly the Bushy-crested Jay (*C. melanocyanea*), the northern form of the San Blas Jay (*C. sanblasiana nelsoni*), and the Yucatan Jay (*C. yucatanica*), were already known to be highly social and to exhibit cooperative breeding (Hardy 1976, Raitt and Hardy 1976). Scattered literature reports and some casual field observations had indicated that the Beechey Jay was much less social than its close relatives, and it seemed, therefore, of importance to examine its social system, the adaptive basis of the system, and its relation to population structure and dynamics.

The project is a continuing one; we expect to obtain additional results based on birds already marked, but the basic outlines of the nature of the social system are already evident. In this paper we describe and analyze some aspects of that system, reserving for a later report details of the population ecology.

STUDY AREA AND METHODS

Field studies on the jays centered on the essential matters of locating nests and observing activity at them and of capturing and marking the birds. The jays are shy, relatively quiet, and difficult to observe and follow in the dense forest. We attempted to bait them to live-traps (both walk-in and bal chatri types), but with little success. We captured 28 fully grown individuals, most in mist nets placed near active nests. Most of the 33 young birds marked were captured by hand, either in or near nests. Colored plastic markers (Raitt and Hardy 1976) in distinctive combinations were applied to both legs of each captured bird. In addition, in 1975 and 1976 matching colored plastic leg bands were applied. Age determination of birds seen or captured was based on color

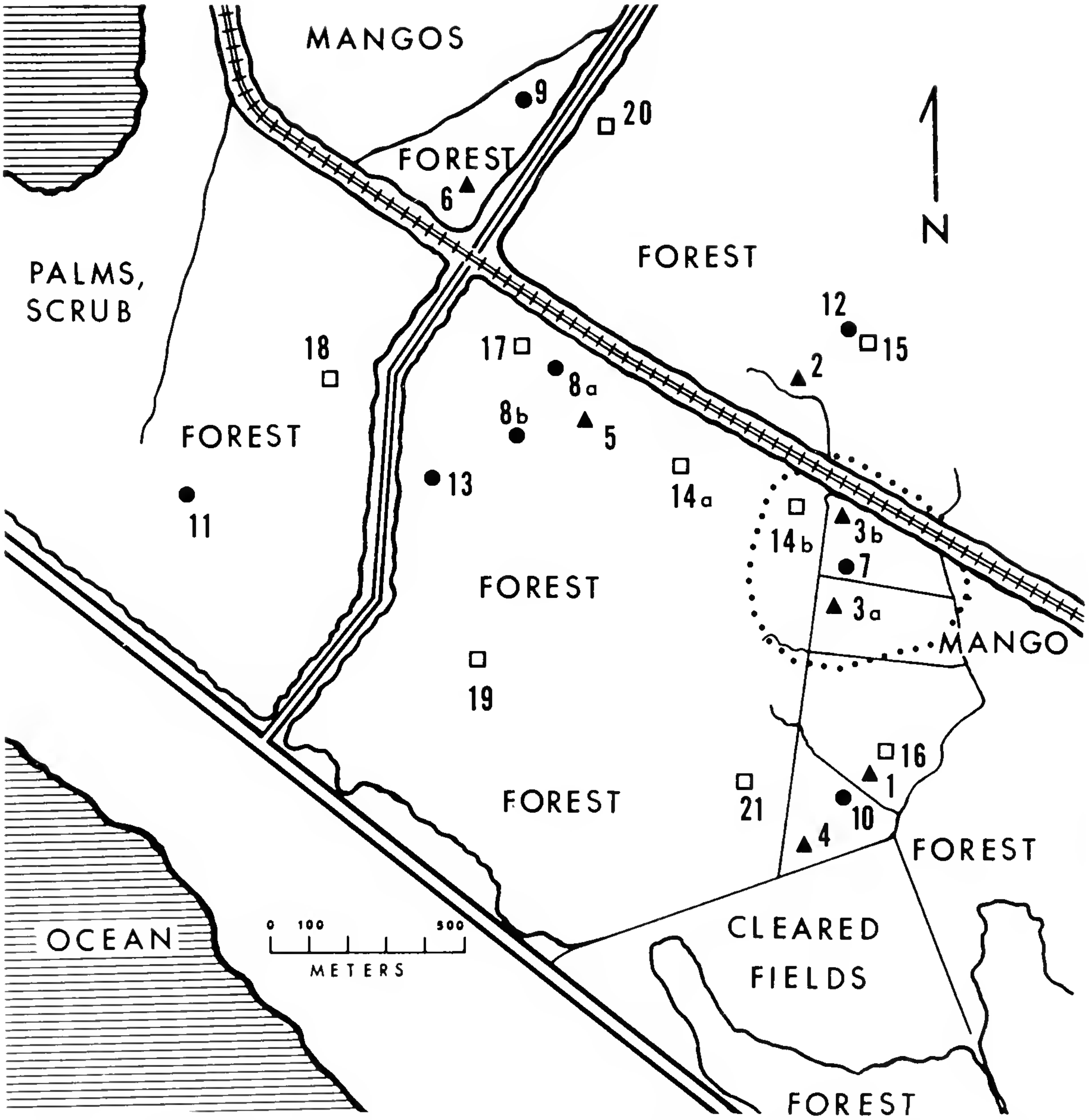

Fig. 1. Principal features of study area approximately 6 km north of Mazatlán. Closed dotted line indicates approximate boundary of observed home range of group B, 1974–75. Numbered symbols indicate locations of nests in 1974 (triangles), 1975 (circles), and 1976 (open squares); lower case letters indicate sequential nestings of the same group in a given year.

of bill and eye, following Hardy's (1973) criteria for recognition of yearlings, 2-year-olds, and adults (birds 3 years or older) (see frontispiece).

For indications of diet, 12 individuals in 1974 and 2 in 1975 were shot in places well away from the main study area. Stomach contents were preserved for analysis in the lab.

Vegetation of the study area was analyzed by means of a system of circular plots, each 100 m^2, using methods modified from those described by James and Shugart (1970) and like those used on our Yucatan Jay study area in Campeche (Raitt and Hardy 1976). The 15 plots were placed in a random-stratified manner, 12 in the main portion of the area, and 3 in the lesser portion northeast of the railroad tracks (see Fig. 1). Within each we measured DBH of each woody stem 2.0 cm or greater in DBH, counted smaller woody stems (designated as shrubs or vines) in 2 randomly located 81° sectors (combined area per plot = 45 m^2), and made cover measurements and notes on foliage, flowering, and fruiting.

Our study area was near Mazatlán, Sinaloa, México. This locality is the approximate center of the species' geographic range, which extends along the coastal plain from southern Sonora (vicinity of Alamos) to northern Nayarit (near Sauta, north of San Blas) (Miller et al. 1957). Dates and degree of field effort are as follows: 4 June–14 July 1974, 6 workers, 177 worker-days; 28 December 1974–3 January 1975, 3 workers, 21 worker-days; 7 June–25 July 1975, 7 workers, 158 worker-days; 29 November–3 December 1975, 3 workers, 15 worker-days; and 24 May–25 July 1976, 9 workers, 193 worker-days.

The study area consists of a tract of deciduous forest that seems to represent optimum habitat, approximately 6 km north of Mazatlán (Fig. 1). The topography is relatively flat, with shallow, dry gullies, except for 2 clusters of small hills that rise perhaps 50–100 m above the general level of the coastal plain. The wide-ranging habits of the jays and their generally sparse occurrence necessitated progressive enlargement of the study area, to over 300 ha, including virtually all of the forested area southwest of the railroad and a sizeable strip northeast of it (Fig. 1).

Data on weather at Mazatlán for 1951–1960 are presented in U.S. Dept. Commerce (1965). Winters are typically dry and mild in temperature (mean for January and February = 20°C); summers are wet and hot (mean for July–September = 28°C). The mean annual rainfall was 805 mm. This amount is not strikingly different from the mean of 1025 mm at our Yucatan Jay study area in Campeche (Raitt and Hardy 1976), but the dry season is much longer and more severe at Mazatlán. In 8 of 10 years there were 6 or 7 months per year with less than 5 mm of rainfall, whereas in Campeche under 2 months had less than 5 mm of rainfall. Beechey Jays and their associated organisms must be adapted to the unfavorable conditions imposed annually by a 6-month period virtually without precipitation.

Except for trails, roads, the railroad right-of-way, and some fields and orchards at the margins, the area is homogeneously forested. Some of the important characteristics of this forest are shown in Table 1. The high densities of woody plants and the relatively low stature of the canopy are likely reflections of cutting. Selective cutting, primarily for fence posts, appears to continue unabated. The values in Table 1 are for all species combined. The most important tree species is *Trichilia trifolia*, which accounted for 46% of the density and 33% of the basal area on our plots and occurs on 13 of the 15. Other important trees were *Zizyphus amole, Guazuma ulmifolia, Ceiba acuminata, Tabebuia rosea, Morisonia americana*, and *Caesalpinia eriostachys*. A species of *Cochlospermum* and 1 of *Ficus* were represented by conspicuous individuals in the area, but were not sampled on our plots.

On a recent large-scale vegetation map of México (Flores Mata et al. 1971) the forests of the region are classified as low deciduous forests (selva baja caducifolia), and our observations confirm their deciduous character. In mid-June 1974, near the end of the dry season, only a few trees bore green leaves; the only species appearing to be fully leafed were *Zizyphus amole* and the *Ficus*; although most of the *Trichilia* bore a number of leaves, none of them was bright green and most were yellow or brown. June 1976 was similar, but in June 1975, the dry season had been less severe and more leaves were green and a few more trees and a small number of shrubs were leafy. Within 2 weeks of the onset of frequent, substantial rains, on 20–21 June 1974, 5–6 July 1975, and 14–15 June 1976, the character of the vegetation had changed markedly; nearly

TABLE 1

SUMMARY OF VEGETATION CHARACTERISTICS OF THE BEECHEY JAY STUDY AREA

	Mean	Range
Trees		
Density (no. per 100 m^2)	61	32–119
Basal area (cm^2 per 100 m^2)	1291	576–2101
Height of canopy (m)	7.5	6–10
Shrub-vine density (no. per 100 m^2)	168	84–420

all of the trees and shrubs were fully leafed and heavy herbaceous growth had appeared on unshaded ground. Reflecting this change the mean canopy cover value for the sample plots changed from 51% in June 1974 to 73% in July. Flowering and fruiting were not heavy, widespread, or absent, during any of our field work, but they were most common in our winter visits to the area.

SOCIAL STRUCTURE

Groups.—The sizes and composition of the breeding groups in the study population are indicated in Table 2. The basic social unit appears to be an adult male-female pair, with or without 1 to 3 additional fully grown birds. The mean size of 20 groups was 3.4 individuals. Ages of the birds accompanying the nucleus pair differed among groups, but yearlings predominated over adults and 2-year-olds. In no case did we detect more than 1 other adult. One exception to the rule of a nucleus pair of adults was group C in the breeding season of 1974, in which the nucleus female was a 2-year-old. Group sizes seemed to increase from 1974 to 1976, but data are too few for statistical confirmation.

In the breeding season, when most of our observations were made (May–August), these groups appeared to be cohesive and stable in membership. Except for individuals actually attending nests, members remained together most of the time and, as will be described later, all members participated in the care of nestlings. In these respects the groups were similar to the generally larger ones characteristic of related species (Hardy 1976, Raitt and Hardy 1976).

Less intensive study in winter indicated that groups retained their integrity in the non-breeding months and that young-of-the-year remained with the

TABLE 2

COMPOSITION OF BREEDING SEASON GROUPS OF BEECHEY JAYS

Group: Nests:	A 1, 4, 10, 16	B 3A, B, 7, 14A, B	C 5, 8A, B, 17	D 2	E 12,15	F 6,9,20	G 13	H 11,18	I 19	J 21
1974										
Adults[1]	2	3	2	2		2				
2-year-olds	0	0	1	0		0				
Yearlings	0	1	0	0		0				
Total	2	4	3	2		2				
1975										
Adults[1]	2	2	2		3	2	3	2		
2-year-olds	0	1	0		0	0	0	0		
Yearlings	1	2	0		1	0	2	2		
Total	3	5	2		4	2	5	4		
1976										
Adults[1]	3	2	2		2	3		3	3	2
2-year-olds	0	2	0		0	0		1	0	1
Yearlings	1	1	1		0	2		0	0	1
Total	4	5	3		2	5		4	3	4

[1] Adults were all birds 3 years old or older (see Hardy 1973).

parental group for at least several months after fledging. Study of groups with individually marked birds indicated considerable stability in group membership and home range from season to season and also from year to year. There was some evidence of interchange of members between groups and of the dissolution of groups. Changes in numbers of breeding groups from year to year (Table 2) partly reflect this instability but also reflect variations in scope and intensity of our field effort.

Movements, home range, territory.—Data on the size of home ranges were derived from watching birds, especially of group B. The area outlined in Fig. 1 is close to 25 ha. In 1976 group B shifted its home range somewhat to the NW and enlarged it to perhaps 30 ha. Sightings of known individuals of other groups were too few to attempt similar estimates. If it is assumed that locations of nests reflect distributions of home ranges and that distances between nests reflect sizes of home ranges, then the mean distance between nests of adjacent groups might be a reasonable estimate of the mean diameter of the home ranges. This mean inter-nest distance in 1974 was 558 m

(N = 5), giving an areal estimate of 24 ha; in 1975 the nests were more dispersed and the comparable figures are 660 m (N = 6) and 34 ha; comparable figures for 1976 were 540 m (N = 6) and 25 ha. A third approach is to divide the total study area—i.e., that total area used by the known groups—by the number of groups. In 1974 6 groups occupied about 110 ha, for a mean area of 18 ha; in 1975 the 7 known groups occupied about 300 ha for a mean of 43 ha; in 1976 the 8 groups in a similar area averaged 38 ha per group. Considering the large size of the study area and the difficulty of observing the birds, the degree of agreement among these estimates is satisfactory.

The question of whether the home ranges are territories, defended against members of neighboring flocks, is of some importance. The use above of inter-nest distances and mean of total area occupied to estimate home range sizes assumes that groups occupy exclusive home ranges. If that assumption were true then the likelihood of territoriality would be high. All of our observations of marked birds suggest that the home ranges were exclusive or nearly so. Furthermore, the agreement between the estimate from sightings of the home range of group B and the estimates derived under the assumption of exclusive ranges is supportive. Finally, we have observed a number of instances of hostile interactions between birds of different groups that suggest territorial defense. Two of these were at the same site. 1 in winter and 1 in summer. This area is near the empirically determined boundary of group home ranges. Both involved aggression near an especially abundant food source, a pile of discarded tortillas in one case, a *Ficus* tree in heavy fruit in the other. In summary, the groups appeared to occupy home ranges of 20–40 ha, that were more or less exclusive to those of other flocks and were defended against members of the other groups.

Mobility within the home range was high. Individuals and groups seldom spent long periods at restricted sites (except the nest), moving from point to point freely, often in no discernible pattern. Often, flights of more than 100 m were made. Most of the time the birds kept to the forest. Special sources of food such as the mango orchards, railroad right-of-way, and highway shoulders where human garbage was dumped did attract birds from the forest, at times for protracted periods; otherwise they remained within it to forage, roost, rest, and nest.

NESTING

We did not study Beechey Jays in the prenesting period; in all 3 years nesting was well underway at the time of our arrival in early June, weeks before the end of the dry season. By back-dating, assuming an 18-day incubation period and a 25-day nestling period, we deduce that laying was completed in early nests on the following dates: 19 and 27 May 1974, 2 on 22 May 1975, and 17 and 24 May 1976. Among Hardy's (1974) captive birds, courtship began in January and February and first attempts at nest-building occurred in April. The latest laying dates in Sinaloa, 9–11 July 1974, were in a known second nesting. In the captives molt became heavy in September and nesting activities ceased.

No exceptions were found to the rule that each group had only 1 active nest at 1 time. We know from direct observations that group B in 1974 and 1976 and group C in 1975 began second attempts after earlier ones had failed. For groups A, C, and D in 1974 we have indirect evidence that they made second attempts, for in spite of failure of their first attempts, they were accompanied in winter by birds of the year.

Nests were disorderly piles of dry sticks with a finer lining, resembling those of other species of *Cissilopha.* The mean height above ground of 15 nests was 5.5 m (range of 4.0–7.6). A large proportion were well concealed in the *Zizyphus* which is evergreen, or *Trichilia trifolia* many of which retain their dead leaves throughout the dry season.

Our data on clutch-size are fragmentary because in over half the nests hatching had already occurred before they were discovered and in many of the others incubation was well advanced. Of nests with incubation in progress, 5 contained 5 eggs when discovered, 1 contained 4 eggs, and 4 contained 3 eggs. It is possible that some of the nests had suffered losses of 1 or more eggs prior to discovery. In the single nest at which we were able closely to follow laying, the clutch was 3 eggs.

ATTENTIVE BEHAVIOR AND COOPERATION

Observations of activities at nests in all 3 years provide data to document and describe the form and degree of cooperation of group members in attending nests; and the following discussion will stress that cooperation, giving little emphasis to other aspects of attentive behavior.

Nestbuilding, incubation, brooding.—Data on nestbuilding were derived from observation of the activities of group B, which was discovered to be in the late stages of constructing nest 3B on 4 July 1974. All of the birds were marked prior to that date, but heavy foliage made observation difficult, and birds were not identified on many visits. All 4 of them visited the nest during construction. At least 3 of them worked at shaping the nest from a sitting position in the nest, but the adult female (PP) did most of this, particularly in the final stages. More than 1, and probably all, brought nesting material.

Nearly all of our data on incubation was obtained at nests 2 and 8B, each attended by an unaided pair. Apparently all of the incubation was done in each case by 1 bird, judged by the presence of an incubation patch to be a female. At both nests the male (the same individual, OO, in the 2 different years) fed the incubating jay at irregular and infrequent intervals. On about half of the occasions when the female left the nest, the male "guarded" the nest from the rim or nearby for a portion of her absence.

Brooding, which was frequent early in the nestling period and ceased on about the tenth day, was likewise performed by a single individual, the nucleus female in all instances when the identity of the brooder was known. As with incubation, on some occasions when the brooder left the nest another member remained to watch the nest.

Feeding of nestlings and fledglings.—For all 10 nests at which feeding of nestlings was observed for more than brief periods, all members of the respective groups participated in the feeding. At 3 others observed briefly, all either fed nestlings or mobbed observers. Because of the high percentage of marked birds the data on the division of labor within group B in 1974 and 1975 are the most detailed for any of the larger groups; they are presented in Table 3. Obviously all members contributed significantly, though contributions were not equal. In both nestings the female parent PP contributed less than others.

Groups at nests 9 and 10 exemplify the division of labor at nests with fewer attendants. The members of the unaided pair at nest 9 brought food the same number of times (21 vs. 22). At nest 10, where a yearling aided a nucleus pair, the 77 observed feedings were approximately equally divided among the 3 attendants.

Food brought to a nest with nestlings being brooded or with another bird guarding it was on some occasions passed to the attending bird. Usually on such occasions both birds then fed the nestlings.

With variation from 2 to 6 in the number of individuals bringing food for nestlings, there was possible variation in feeding rates correlated with the number of feeders. Comparable data are few and conclusions are ambiguous. Nests 7 and 10 were comparable in timing and each contained 3 nestlings, but nest 7 had 5 attendants while nest 10 had 3. For comparable periods we recorded 50 feeding visits in 10.7 h of observation at nest 7, for 4.7 visits/h, and 64 feedings in 14.7 h, 4.3/h at nest 10. The difference between these rates is negligible. On the other hand, in a similar comparison between nest 7 and nest 9, which was attended by only a pair, the rates were 4.5 and 3.2, respectively.

On 30 June 1974 the single youngster in nest 6 fledged. For the next 2 days this fledgling was sufficiently sedentary to allow prolonged observations

TABLE 3

PERCENTAGES OF FEEDINGS OF NESTLING BEECHEY JAYS BY DIFFERENT MEMBERS OF GROUP B AT NEST 3A (1974) AND NEST 7 (1975)

Nest 3A (74 feedings) Individual:	PP, nucleus female	WV, nucleus male	AA, adult female	GG, yearling	
	11	36	16	36	
Nest 7 (89 feedings) Individual:	PP	WV	GG	OG, yearling	PV, yearling
	18	26	21	10	25

of its activity and that of its attendants, an unaided pair. In a combined period of 4.8 h it was fed 26 times, a rate of 5.4/h, which is higher than we have observed for nestlings. One or the other parent was frequently nearby, but they seemed not to make a special effort to accompany the juvenile. The male attendant made over twice as many of the feedings as the female. In addition to the visits when food was actually delivered to the youngster, there were 10 visits in which parents attempted to feed, but left when the youngster refused to open its mouth. By the second day out of the nest the fledgling had become quite mobile, and by the third day attempts to find it were unsuccessful even though it was still alive, as we discovered the following January.

FOOD AND FORAGING

Analysis of stomach contents gave the following results: mammals (1 possibly *Reithrodontomys*) in 2 of 11 stomachs; lizards (*Anolis* and other, unidentified) in 2; Coleoptera (including at least Curculionidae and Cerambycidae) in 9; Lepidoptera (larval Geometridae) in 2; Orthoptera and spiders in 1 each; snails in 3; and seeds (corn, oats, and other, smaller ones) in 8 of 11. Observations of birds foraging or carrying food extend the variety. They include 5 instances of capture of lizards, including the common *Anolis*, and 3 additional ones of delivery of lizards to nestlings. Invertebrates captured or delivered include mosquitoes, winged termites and ants, cockroaches, cicadas, adult Lepidoptera of several kinds, many unidentified insects, and, especially, geometrid larvae, of which there was an outbreak of large numbers for about a week soon after the onset of rains each year. Vegetable material seen eaten includes waste grain along the railroad, corn on the ground or on stalks in cornfields, mangos from both trees and ground in orchards, immature fruit at the bases of flowers of

Ceiba trees, wild figs, a variety of berries from trees and shrubs, and tortillas from trash dumps.

Sites and modes of foraging also were varied. Foraging occurred within the forest and at its edges, in cornfields, mango orchards, and along the railroad right-of-way. Approximately equal numbers of our observations of foraging were of birds on the ground and in trees, with a lesser number in shrubs. Individuals foraged in all portions and levels in trees. They picked lizards, invertebrates, and fruit from foliage and branches; probed in cracks, under loose bark, into epiphytic bromeliads, into leaf litter on the forest floor; and even hawked after flying termites.

DISCUSSION

The findings presented in this paper have some significance in our overall comparative study of the sociobiology of the several forms of *Cissilopha*. Table 4 summarizes the salient features of *C. beecheii* that are shared with the other forms and the important differences. Data for the comparison are from Hardy (1973, 1976), Raitt and Hardy (1976), and a concurrent study of *C. s. sanblasiana*. Comparative characteristics of other forms stress those of *C. yucatanica* and *C. s. sanblasiana*—especially where there is variation apart from that involving *beecheii*—because we know more about the ecology of their social systems than those of *C. melanocyanea* and *C. sanblasiana nelsoni*.

Similarities between *beecheii* and the other forms are numerous and include important features of their ecology and breeding biology. They support the usual conclusion based on morphology and other taxonomic characters that *beecheii* is closely related to the others, and indicate that it occupies a generally similar niche. The differences are more interesting, for they are more numerous and more striking than the differences among the other forms. Of these differences it is highly likely that the lower degree of sociality, the fewer nests per group, and the low density are interrelated and are adaptive responses to a harsher environment than that occupied by the other forms of *Cissilopha*. As pointed out earlier, the climate in which the Beechey Jay lives is more xeric than is the range of the Yucatan Jay, and perhaps more importantly, it is characterized by a longer, more severe dry season, averaging over 6 months. Differences in the vegetation and well known regional variations in climate indicate that the ranges of the San Blas and Bushy-crested jays are likewise less xeric and less seasonal than that of the Beechey Jay. We postulate that the climatic regime of the latter results in generally lower and highly seasonal productivity of food resources, which would thus simply not support the

TABLE 4

SUMMARY OF SOME SIMILARITIES AND DIFFERENCES BETWEEN *C. BEECHEII* AND OTHER FORMS OF *CISSILOPHA*

Feature	Comments
Similarities	
age differences in phenotype	—3 recognizable classes in fully grown birds
breeding season	—begins in dry season (May), extends into wet season (July–August)
nests (see also below)	—structure, placement similar in all forms
eggs	—shape, size, color similar in all forms
incubation, brooding	—1 bird does all or nearly all, except often 2 in *melanocyanea* and *sanblasiana nelsoni*
spatial structure	—groups with stable, probably exclusive, ranges
cooperation	—(a) group helps during nest construction
(see also below)	—(b) incubator-brooder attended, nest guarded (extent variable)
	—(c) all members of group feed nestlings and fledglings (?)
Differences	
body size	—*beecheii* larger: mean body wt. = 195 g; *yucatanica*: 122 g; *s. sanblasiana*: 111 g
breeding season groups	—smaller: 2–5; average about 12 in others and none normally as few as 3
cooperation	—greater division of labor in some forms
nests	—no overlap in attempts in *beecheii* but always in others; 2 or more potentially successful in others, only 1 in *beecheii*
density (biomass)	—low: ca. 10/km^2 (1.95 kg/km^2) in *beecheii*; ca. 70/km^2 (8.54 kg/km^2) in *yucatanica*; ca. 170/km^2 (18.87 kg/km^2) in *s. sanblasiana*
diet	—varied, omnivorous in all; vertebrates more common in *beecheii*
habitat	—*beecheii* more dependent on forest; others prefer edge or open forest or plantations; *beecheii* habitat more xeric

locally heavy trophic demands of the large social concentrations and multiple nests characteristic of the other forms.

The causal relationships involving large body size are less clear. Large body size makes high sociality less likely, in terms of the ability of the food supply of a given area to support a given biomass. But large size may itself be an adaptation to a reduced food supply. Large size may seem to be a specialization within *Cissilopha*, but it may in fact permit a more generalized diet. Schoener (1971) points out that "unless food supply is very abundant, larger animals should . . . usually eat a greater range of food sizes than smaller ones," and Wilson (1975) has recently presented data for several groups of birds which confirm the fact that larger species eat a broader size range of food items. Such seems to be the case with *C. beecheii*: its diet includes the same sizes of seeds and arthropods as that of *C. yucatanica* but it also eats a substantial number of vertebrates, which the smaller jays would have more difficulty in capturing and handling. The postulated adaptive advantage of the more generalized diet in an area of seasonally low food supply is that the vertebrate prey may be a resource to be relied upon when food is scarce and needs are great, whereas smaller food items and fruits, supplies of which are characteristically highly abundant but temporary, may be capitalized upon at other times. Because these other food items are often locally abundant—e.g., termite and ant swarms and fig-laden trees—it is feasible in the sense of time-energy budgets for the larger jays to include them in their diet even though individual items may be small. It is also possible that body size is related to inter-specific selection pressures (Schoener 1971, Cody 1974), but this is an unlikely explanation for the larger size of Beechey Jays because their most likely competitors, the Mexican Crow (*Corvus imparatus*) and Magpie Jay (*Cyanocorax formosa*), are both at least as large as they are. Diffuse competition remains an elusive possibility.

Two additional important questions arise as a result of the previous discussion: (1) In view of the above arguments concerning low sociality in Beechey Jays, what is the advantage of the existence of the larger groups with a degree of social cooperation? and (2) In a proximate sense, how are the groups kept small, in the face of apparently strong social tendencies? The first of these questions is a portion of one of our primary questions in originally undertaking comparative study of this group of jays; it can be better approached in the context of the 4 species, with data from additional field study, especially concerning reproductive success of pairs vs. larger groups. As for question 2, Hardy (1974) presented evidence from study of a few captive birds that, in confined situations of cage or aviary, an adult male of a mated pair was strongly intolerant of another adult male. When the latter was placed in a cage with the pair, it was severely pecked and would have been killed had it not been removed. So long as it was in sight of the male, however, that individual remained in an aggressive state, directing threat postures and pecking toward the other male. As mentioned previously, yearlings predominate as helpers, and never more than 1 adult has yet been recorded as a helper in one of our groups. Thus the groups may be kept small by the intolerance of the nucleus male toward other adults. As yet, we do not know the sex of these adult helpers. It is possible that group size may be limited without social interactions, through a balance of reproduction and death. Such limitation would appear to require independent density-dependent effects on each group, perhaps a less likely possibility than the operation of social exclusion of the sort observed in captive birds.

CONSERVATION STATUS

The Beechey Jay is a distinctive Mexican endemic with a restricted geographic range. It occupies a habitat the existence of which is precarious in the face of growing human population and agricultural development. In a major portion of its range, north of Culiacán, Sinaloa, into southern Sonora except along certain rivers, the deciduous forest has been virtually replaced by pasture and cropland. Our experience in the last decade is that clearcutting of the Beechey Jay's woodland habitat is accelerating. Earlier, when simple handheld tools were used merely to prune out small tree trunks, the woodland still maintained its basic character. Our entire study area is clearly second growth and seemingly when in this form remains good habitat for the jay. We have seldom, however, observed the jay where the forest has been severely changed in structure or removed. Although Beechey Jays may forage briefly in open areas adjacent to forest, unlike their close relatives they prefer more than forest edge, always retiring to the interior for most of their activities, including nesting. Consequently, we judge the Beechey Jay to be threatened and perhaps endangered by standards currently applied by governments and conservation agencies. The jay's extinction seems possible within the next few decades if habitat destruction continues at its present pace.

SUMMARY

We studied the Beechey Jay most of 3 breeding seasons and in 2 short non-breeding periods near Mazatlán, Sinaloa, México. We color-marked 28 fully grown birds and 33 young. The Beechey Jay lives in low deciduous forest, mostly second growth, on the coastal plain and low rolling hills of western México from Sonora to Nayarit. Near Mazatlán, the dry season usually extends from November into June.

The jays live year round in social groups of 2–5 individuals ($\bar{x} = 3.4$). The basic unit seems to be an adult male-female pair; birds accompanying the pair range from yearlings to adults, but yearlings predominate. Groups are relatively stable, but some shifts occur in membership from year to year.

Group home ranges were 24 to 43 ha and seemed virtually exclusive, suggesting territoriality, as did hostile interactions between birds of different groups near the empirically determined home range boundaries. Mobility within the range was high, and birds could be seen regularly only near nests. Beechey Jays are largely birds of the forest interior, venturing to the edge or the open only briefly to forage, usually in early morning or late evening.

Groups had no more than 1 successful nest per year; an early unsuccessful attempt was soon followed by a second attempt. Nesting began in the dry season in early May (completed clutches known from 17 and 19 May). Latest laying dates were 9–11 July, presumably in second nestings. Nests were disorderly piles of sticks with a finer twig lining, placed an average of 5.5 m up, usually in trees that had retained some foliage, such as *Zizyphus* and *Trichilia.* All group members helped in nest building, with the adult female of the nucleus pair doing most of the construction. Incubation and brooding were solely by this female, who was attended mostly by her mate. When the female was off the nest another bird usually remained as a "guard" nearby or on the rim of the nest. Five eggs were the most common clutch-size; smaller clutches may have resulted from predation.

All group members fed the young, all contributing significantly. Between 4 and 5 feeding visits to the nest/h was typical for groups with helpers; at 1 nest where only a pair attended the young the average was 3.5 visits/h. A single fledgling was fed 5.4 times/h, though there were other visits when the young would not accept food. By the second day out of the nest a fledgling was quite mobile. Though still alive, it was not locatable on the third day.

Beechey Jays have an extremely varied diet including small seeds, fruits, insects, lizards, and mice. Sites and modes of feeding were varied; besides the forest, from ground to canopy, jays took food on a railroad right-of-way and in orchards. They probed bark, gleaned foliage, searched leaf litter, and hawked insects.

Similarities in morphology and behavior indicate a close relationship between the Beechey Jay and other black-and-blue Jays. However, the ways in which it differs are interesting. It seems to be a form whose differences represent responses to a more arid, more highly seasonal environment. The lower degree of sociality, fewer nests per group, and low density are apparent responses to reduced and/or less predictable food supply in a less productive habitat. Large size may be related to this pattern, being itself an adaptation to reduced food resources. Recently certain authors have postulated that among related bird species, larger ones eat a broader size range of items. Small group size may be the result of intolerance of the nucleus male to other adults (males only?) but field evidence is lacking.

The Beechey Jay should be regarded as threatened or endangered, since it requires forest and its habitat is being clearcut and put to grazing and agricultural use, as well as encroached on by human populations.

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BURDENS OF THE PICID HOLE-EXCAVATING HABIT

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Woodpeckers (Picidae, some 200 species) are well known for their woodpecking, drumming, and other habits, but obviously their ability to excavate their own nesting and roosting cavities in wood, sometimes well-rotted, but often in sound wood, is of major importance in their biological "success." That the hole-nesting habit is advantageous is evident not only from the wide distribution, relative abundance, and number of species of woodpeckers, but from the great number of species of other bird families that are unable to excavate their own cavities, and seize upon every opportunity to avail themselves of woodpecker holes. Indeed, some species in at least some situations are so dependent upon woodpecker holes that their abundance and distribution may be affected by the occurrence and availability of such nesting sites; immediately to mind come such American species as the Tree Swallow (*Tachycineta bicolor*) various species of *Myiarchus* flycatchers, and the Elf Owl (*Micrathene whitneyi*) and Old World species such as flycatchers of the genus *Ficedula*, many starlings of diverse genera, and pygmy owls, genus *Glaucidium*. Von Haartman (1971) demonstrated that the population density of hole-nesting birds could be dramatically increased by providing nesting boxes where holes were uncommon or lacking in managed forests. and he showed that such birds are substantially more numerous in unmanaged forests that have holes available than in similar, but managed forests. Holes are so much in demand that the woodpeckers are under heavy pressure from 1 or another species that tries to usurp their cavities from the moment the woodpecker excavation reaches the point of usability (see Tracy 1933:118–119, Szlivka 1957, 1960, Blume 1968, Kilham 1968, 1969, 1972a:37).

It is important to note several points about woodpeckers and their holes. Virtually all picids require individual roosting cavities (Blume 1968, Short 1974a, in press). and these usually are in separate trees. Sometimes woodpeckers may roost outside holes. if none are available. but the prevalence of widespread, year-round excavation of new holes for roosting suggests that the birds are safer in holes. hence it is selectively advantageous for them to have a roosting hole. Further, individuals may have several alternate holes (Blume 1968): they may switch occasionally. and can do so if a cavity is lost, or they are frightened and forced to evacuate a cavity. Based upon my experience with over half the woodpeckers of the world (see, e.g., Short 1971a, 1973, and also such works as Blume 1962, 1968), most species excavate a new nesting cavity yearly. The male of a pair often shifts from his roosting cavity to the nest for roosting after it is fully excavated (he may shift back again to the prior hole after nesting, see discussion of *Picoides leucotos* in Blume 1968). It follows that ideally each woodpecker territory should have a number of available holes and certainly a number of trees suitable for excavating holes. Ideally there should be several alternate roosting holes per bird. The availability of numerous holes is especially advantageous after the young of the year are fledged, for fledglings are particularly vulnerable (see Blume 1968:54) until the time when they can excavate their own cavities. The presence of suitable, unoccupied cavities for roosting probably enhances survival of the young birds during this crucial phase of life. Finally, it follows that the unavailability of trees suitable for excavating holes, or the occupation of woodpecker holes by other animals may influence the suitability of a territory for a woodpecker pair. Pressures caused by lack or occupancy of holes may be varied, and subtle. For example, the female of a nesting pair presumably must have a roosting hole on or near the territory of her mate—loss of her roosting cavity, if suitable trees for excavation are at a premium, conceivably could interfere with breeding activities, even rendering nesting impossible, if, for example, she was forced to roost too far from the nest to reach it readily. A scarcity of trees suitable for excavating presents a problem compounded by competition for the existing, already excavated holes in an area.

I here review some of the problems woodpeekers face in competition for their nesting and roosting holes, and I treat the adaptations of the woodpeckers to overcome or minimize these problems.

COMPETITION FOR NESTING AND ROOSTING SITES

Woodpeckers seem to "recognize" potential nest-competitors, perhaps through experience, and to distinguish such nest-competitors from species that do not pose this threat. Intense reactions may occur, as between Black-backed Woodpeckers (*Picoides arcticus*) and Tree Swallows (Short 1974b), throughout the breeding season, even when there is no direct threat to the nesting hole. The Black-backed Woodpeckers attack Tree Swallows that perch anywhere in the vicinity of the former's nest (they also attack individuals of *Colaptes auratus*, *Sphyrapicus varius*, *Picoides villosus* and *P. tridactylus*), and in turn the Tree Swallows attack and harass any Black-back that chances to land in a stub in the open where Tree Swallows are foraging in numbers. On the other hand, if sufficient cavities are available, woodpeckers may nest very close to competitors that are tolerated with little or no interaction (see, e.g., Eates 1937, Hoyt 1957, Szlivka 1960, Skutch 1969, Reller 1972).

The introduced Starling (*Sturnus vulgaris*) has spread across the North American continent partly at the expense of non-picid hole-nesters such as the Eastern Bluebird (*Sialia sialis*), and probably with some detrimental effects on woodpeckers such as the Northern Flicker (*Colaptes auratus*) and Red-headed Woodpecker (*Melanerpes erythrocephalus*), although it mainly uses natural cavities in trees, human edifices and structures, and old, abandoned woodpecker holes. Well-adapted by its sheer persistence to evict woodpeckers and other birds, Starlings win many although not all battles for woodpeckers' holes (see, e.g., Bent 1939, Szlivka 1957, Stickel 1963, Kilham 1968). The severity of the competition is indicated by occasional death of woodpeckers or Starlings in their conflicts over nest-sites (Shelley 1935).

Other non-picid competitors may or may not be as aggressive as Starlings, but usually show persistence in their efforts. The tityras (*Tityra semifasciata* and *T. inquisitor*, Skutch 1969) are successful in usurping nests of several melanerpine woodpeckers by filling the woodpeckers' holes with leaves and debris whenever the woodpeckers are absent; the latter eventually may give up removing the leaves and abandon the nest. Skutch (1969) also noted the aracari toucans (*Pteroglossus* sp.) as severe competitors for the holes of woodpeckers, and they may prey upon young woodpeckers as well. Tarboton (1976) indicated his strong suspicion that Crested Barbets (*Trachyphonus vaillantii*), a competitor for holes occupied by wrynecks (*Jynx ruficollis*) in South Africa, may kill the young wrynecks if there are young in the nest when they commence their takeover. Not only toucans and barbets, but other tropical birds such as parrots, hornbills, and even some ovenbirds (*Xenops*) and dendrocolaptids (fide P. O'Brien) often usurp woodpecker nests, and owls and hole-nesting falcons may do so. Mammals such as flying squirrels and other squirrels, monkeys, and others evict woodpeckers (and other hole-nesting birds) from holes they have excavated or occupied. Predatory mammals and snakes may eat the eggs or young of woodpeckers, then settle for a time in the nesting cavity.

The intensity of competition for newly excavated holes may be greater than that for older cavities since the former are clean. Older holes develop a microfauna often including parasites and other vermin that may make such holes less than attractive. Newly excavated holes lack pests, and thus may be preferred by woodpeckers and their competitors. Tracy (1933), Szlivka (1957, 1960), Blume (1968), Kilham (1968, 1972a), and Skutch (1969) provided data emphasizing the takeover or attempted takeover of woodpecker nests just at the point of completion. There are many cases of woodpeckers excavating 2, 3 or even more cavities and losing them just at completion of excavation (see Szlivka 1957, Stickel 1963, Kilham 1968, and Jackson 1977).

The effects upon woodpecker populations of nest losses to the various competitors are difficult to evaluate, and appropriate data are sparse. Troetschler's (1976) studies of the Acorn Woodpecker (*Melanerpes formicivorus*) of western North America, only exposed to Starlings for the past few decades, indicate substantial impact on that woodpecker. Almost all of the nests excavated early in the season (presumably at a time most optimal for the woodpecker) in some areas, are lost to Starlings and consequently the average timing of hatching of young woodpeckers has shifted to later in the season. Flickers may in some areas, be affected similarly, and so too are Great Spotted Woodpeckers (*Picoides major*) in Europe (Blume 1968). Nests excavated by Great Slaty Woodpeckers (*Mulleripicus pulverulentus*) in Malaya were repeatedly usurped, or the woodpeckers driven away, by hornbills or mammals (Short 1973). Thus, the seemingly very long breeding season of this species reported by various authors seems due to the initial, and perhaps repetitive loss of the nest (which may take 3 weeks or a month to excavate, after a suitable site is located—up to 6 or so weeks may be lost if the nest is usurped just after excavation is completed, and even more time is lost if nesting has progressed to the egg-laying, incubation, or nestling period). In the case of repetitive nest-hole losses of woodpeckers to Starlings, mentioned above and involving at least several picids (e.g., *Melanerpes carolinus*, Stickel 1963; *Picoides syriacus*, Szlivka 1957; *P. villosus*, Kilham 1968; and *P. borealis*, Jackson 1977), it is obvious that several re-excavations and new breeding attempts in succession substantially delay nesting, pushing it beyond the presumably optimal period of the initial endeavor. Tropical woodpeckers particularly seem prone to lose their initial nest; Skutch (1969) and Short (1970) treated a number of instances in the Neotropics, Short (1973) discussed some cases in Asian picids, and Short (pers. obs.) has seen losses of Nubian (*Campethera nubica*) and Bearded woodpecker (*Dendropicos namaquus*) nests to various African starlings, and, as noted above, Tarboton (1976) reported that barbets usurp wryneck nests in southern Africa.

Woodpeckers of course are among the potential and actual nest competitors of other picids. (I exclude from consideration intraspecific competition, and competition between allospecies in zones of contact, as this is almost equivalent to intraspecific competition.) Such nest usurption often occurs during the excavation period, 1 woodpecker, usually representing a larger species simply driving away the other, usually smaller woodpecker, enlarging its excavation, and nesting therein. I have seen this in such species as the Hairy to the Downy woodpecker (respectively *Picoides villosus* and *P. pubescens*; see also Kilham 1962). Other examples include enlargement of nests of *Picoides minor* by *P. major* (Tracy 1933), of *P.*

borealis by *Melanerpes carolinus* (Ligon 1971), and of *Melanerpes pucherani* by *Dryocopus lineatus* (Kilham 1972a). The episode described by Tracy (1933) illustrates the intensity of the interaction, for the larger species (*Picoides major*) persisted in enlarging the cavity of *P. minor* despite strong attacks by the latter, and the interference of the human observer on behalf of *minor* (the success of *major* was but temporary, for subsequently it lost the enlarged cavity to Starlings). This competitive pressure may explain the tendency for small picids, especially, to favor sites that barely permit the dimensions of their nesting (or roosting) cavity, i.e., sites that larger species cannot use. Some small species prefer to excavate into the underside of thin branches, as does *Melanerpes rubricapillus* (Kilham 1972a), again in situations unlikely to attract a large woodpecker.

More difficult to understand is the actual enlargement of cavities of smaller woodpeckers by larger picids involving sites that the larger birds either cannot or usually do not use. A White-bellied Black Woodpecker (*Dryocopus javensis*) methodically enlarged an intended nesting cavity of the much smaller *Picus puniceus*, the Crimson-winged Woodpecker, in Malaya (Short 1973). The *puniceus* cavity was in a branch much too small to afford a cavity that could accommodate *javensis*, yet the latter gradually rendered it unsuitable for *puniceus*, enlarging the opening until it was far too big, and the cavity exposed. The larger woodpecker did not feed during its excavating. One could consider this to be a competitive reaction, but there is virtually no overlap or possible direct competition between these picids, either in foraging (feeding modes and sites differ, Short 1973), or in nesting and roosting sites. Dennis (1971) and Jackson (1978) also described the habit of Pileated Woodpeckers (*Dryocopus pileatus*) of enlarging Red-cockaded Woodpecker (*Picoides borealis*) holes that the pileateds only occasionally are able, or choose, to use.

The greatest degree of competition among woodpeckers would appear to be between similarly-sized species, and particularly between similarly-sized congeneric woodpeckers that overlap in foraging habits (see, e.g., *Picoides macei* and *P. canicapillus in* Short 1973); these are apt to have similar nesting requirements as well as similar foraging sites, hence contact between them will be frequent. I have described (Short 1971b) an instance of intense, direct interspecific aggression and territoriality between the usually non-interactive Hairy Woodpecker and Nuttall's Woodpecker (*Picoides nuttallii*) in a situation involving a rather poor, ecologically simple habitat that was, however, abundantly occupied by the smaller *P. nuttallii.* A pair of Hairy Woodpeckers appeared, out of their normal habitat, and were engaged constantly in conflicts with persistent, numerous Nuttall's Woodpeckers, interfering with the Hairy Woodpeckers' endeavors at nesting. The degree of contact may influence strongly the relative competition between woodpeckers for nesting sites. Indeed it is in primary tropical forests with dense, wet vegetation, rendering the woodpeckers difficult to see and muffling the sounds of their workings, that the greatest number (up to 13) of picid species can coexist (Short 1978).

ADAPTATIONS RELATING TO COMPETITION FOR HOLES

Considering the specialization of woodpeckers for obtaining insects below the surface of tree-bark, one might expect that tropical woodpeckers could tolerate the loss of nesting holes rather easily, i.e., they should be able to find insect food in trees, and thus to nest as easily at one as at another time of the year. This might be the case for a few highly specialized "wood-pecking" species, but in fact most picids nest at that time of year when food is most readily available and easily accessible in quantities sufficient to feed and raise their young. Many woodpeckers that feed by excavating much of the time into the bark may nest when certain insects are available at the surface, and forage then by gleaning for insects to feed their young (e.g., 4 sympatric species of *Picoides* in southern California, Short 1971b). Thus, woodpeckers are apt to breed at an optimal time of the year, as are most birds, and this especially is likely wherever there is a distinct or even partial seasonality affecting rainfall, vegetation, and food supply. Temperate zone woodpeckers are strongly seasonal breeders. For most woodpeckers a delay in nesting is apt to be detrimental, hence the ability to excavate and defend a nesting cavity is very advantageous.

Woodpeckers usually become very attached to the nest site as the excavation nears completion, and from that time until the young have hatched and are partly developed, 1 or the other parent usually can be found near the nest. When an adult is within the cavity the chance of a nest-competitor dislodging it from the nest is slim (Lawrence 1967, Kilham 1968, Skutch 1969), but persistent efforts by some competitors often are rewarded once they are able to enter the nest during an infrequent absence of both woodpeckers. Nevertheless constant surveillance of the nest and occupation of the hole by the woodpeckers from the time the nest is completed, though egg-laying, incubation, and hatching periods, until such time as the nestlings can climb to (and thus, by their presence, "protect") the nest entrance, help to reduce nest losses to competitors.

Loss of the nest to competitors that happens despite actions of the woodpeckers to retain it may be followed by rather rapid renesting. This is facilitated by several activities that, if not influenced by selection favoring rapid renesting, at least preadapt woodpeckers for such action. Most picids excavate 1 or more roosting cavities during the course of the year, usually at times other than during the breeding season. Almost every adult woodpecker has 1 or several roosting cavities or evasion holes (Blume 1962, 1968) to which it can retire at night in relative safety. As noted above, once nesting commences the male parent occupies the nesting cavity from the time it is sufficiently complete to make this feasible until the young near the time of fledging. Since the shift of the nesting male from its roosting cavity to the (usually newly constructed in most picids, see, e.g., Blume 1962, 1968, Lawrence 1967) nesting hole frees the roosting site, that cavity is potentially available for renesting. Other roosting cavities of members of a pair also are available for renesting. Such cavities require minimal enlarging or modification, hence the renesting will be much more rapid than would occur if a new cavity had to be excavated.

Furthermore, during the initial period of nest excavation the woodpecker may start several holes before finally deciding on that to be used for nesting. Other partially worked holes usually are found in any woodpecker's territory, leftovers from abortive nesting or roosting hole construction. Some of these may be suitable for full excavation, and to the extent that they have been excavated earlier, time will be saved in renesting (for the importance of such holes see Blume 1968:39 for *Picoides major*, and ibid:75 for *P. medius*). It is logical that hole-working that human observers might interpret as irrelevant behavior or even "play" is selectively advantageous in providing initial holes that, in an emergency (need for roosting or nesting hole) can be completed more rapidly than a new construction.

Seasonal adjustments might be expected as means of avoiding both picid and non-woodpecker competition for nesting sites. There is no evidence that such adjustment occurs in relation to non-picids. As regards woodpecker competition, Kilham (1972b) showed that *Campephilus melanoleucos* and *Dryocopus lineatus*, 2 similar-appearing woodpeckers, nest at different times of the year where he studied them in Panama, but data from juvenile specimens of both suggest some seasonal overlap in Panama, and in Mexico *C. guatemalensis* (a close relative of *C. melanoleucos*) may nest at the same time of year, and even in the same tree simultaneously with *D. lineatus* (Shaughency, *in* Short in press). It is unlikely that very great shifts in seasonality are possible in most picids. Since many woodpeckers are resident. permanently territorial species that may excavate roosting cavities at any time of the year, interspecific contact, and competitive interactions are not confined to the breeding season. For example, competitive interactions between Indian *Picoides maeci* and *P. canieapillus* affect foraging activities whenever the birds meet (Short 1973, 1975). Hence a radical shift in breeding seasons for purposes of avoiding nest-site competition would not seem to accomplish sufficient avoidance or insure that the nesting site would not be lost to picid competitors.

The ability of woodpeckers to excavate cavities in wood is shared by other groups of birds (barbets, kingfishers, parids) only to the extent that the woodpeckers use well-rotted, dead wood. Excavation in live trees having hard wood is advantageous to some extent in reducing nest losses to competitors larger than the woodpeckers that perform the excavation. Non-picids larger than the woodpeckers are unable to enlarge the opening of a cavity (see Lawrence 1967:104) in live or very hard dead wood. Non-picid hole-nesters smaller than woodpeckers, such as tits, some flycatchers and others usually do not offer competition to woodpeckers, except in the case of *Passer* (Szlivka 1960). Competitors that often are successful and pose a serious threat are those larger than the picids, such as falcons, perhaps owls (see Graber et al. 1977:10; owls also are predators of woodpeckers), hornbills, toucans, rollers, and others. It follows that any excavation of a roosting or nesting cavity by a woodpecker ought to be as small as possible to discourage potential predators. There is abundant evidence that the smaller woodpeckers particularly excavate holes with openings as small as possible e.g., pied woodpeckers, Lawrence 1967, Blume 1968; sapsuckers, Lawrence 1967; piculets, Short 1970, in press). Excavations in live wood offer an advantage for the owner even in the case of competition from other woodpeckers in that any enlargement must be accompanied by loud sounds of excavating that are sure to attract the owner's attention, whether or not it can prevent the enlargement. Not only do most woodpecker holes have small entrances, but the woodpeckers excavate, in live trees and hard dead trees, a tunnel penetrating some distance into the wood before dropping down into a chamber. Thus, a potential usurper larger than the woodpecker not only would have to enlarge the entry, but would face the difficult and awkward task of enlarging a section of tunnel through hard wood. In addition to the small entry and tunnel, it is advantageous as well if the stub used is not much larger than that needed for the sized woodpecker involved. Of course small stubs bearing woodpecker cavities are apt to break in storms (see especially Skutch 1969), so the selective advantage accruing from use of a small stub (large nest competitors would find the site unsuitable, but see the above-mentioned cases of enlargement of unsuitable cavities by large woodpeckers) is to some extent balanced by selection favoring choice of a sturdy site to minimize loss of the nest by breakage of the stub.

The particular site of a nest may discourage potential nest-hole competitors. Like many small barbets (genus *Tricholaema*, 3 species, pers. obs.), *Melanerpes rubricapillus* favors sites on the underside of rather small branches for its excavations. Many though not all birds find it difficult to cling to the underside of a small branch, to say nothing of fending off the picid owners, working on the wood from an upside-down position, and carrying nesting material into the nest chamber.

The nesting of many tropical, and some other forest and woodland picids outside the forests or woods (see Skutch 1969, Short 1973), i.e., in isolated trees in pastures or other areas adjacent to woods, not only reduces predation by arboreal predators but also limits nest-hole competition from more secretive forest and woodland species that do not leave these areas. These advantages often seem to outweigh the greater exposure of the isolated trees to wind and lighting, and of the woodpeckers to aerial predators as they fly across open areas to the nesting site. From personal experience I have found (Short in press) that many forest and woodland picids frequently seek out trees standing apart from forests in which to excavate nests. These woodpeckers include even such interior forest birds as Asian *Dinopium rafflesii* and South American *Campephilus melanoleucos,* as well as many other species (divergent examples that come to mind are: *Piculus aurulentus, Veniliornis spilogaster* and *Dryocopus lineatus* from the Neotropics; *Picoides obsoletus, Dendropicos xantholophus* and *Campethera cailliautii* of Africa; and *Picus puniceus, Reinwardtipicus validus,* and *Dryocopus javensis* of Asia). Arboreal competitors (some also are predators) for holes that are excluded from competition by placement of a woodpecker's nest in an isolated tree outside the forest include various mammals (squirrels, monkeys) and also some hornbills, owls and other birds that find that situation unsuitable. Some woodpeckers (as well as other birds) especially may choose trees near human habitation, a situation which excludes certain "shy" or persecuted aerial and arboreal predators and nest competitors (although perhaps adding others, such as non-forest starlings in Africa and elsewhere).

A few picids reduce competition for nest holes by excavating their nesting cavities in occupied ant or termite nests, either raised above the ground or in trees. All the woodpeckers that use these sites subsist to a large extent on ants and termites. Such species are *Celeus brachyurus* of Asia (Short 1973; almost exclusively nesting in termite or ant nests), *Campethera nivosa* of Africa (Chapin 1939) and *Piculus chrysochloros* and *Celeus lugubris* in South America (Short 1970). The nature of the substrate and presence of the ants or termites would seem to deter both predators and thinner-skinned (picids have tough, thick skin) nest-competitors, but not the picid excavators. Studies of the nesting of such woodpeckers are needed to gain data on these matters, but intuitively it seems that relief from such pressures was a factor in the evolution of such nesting habits.

Red-cockaded Woodpeckers (*Picoides borealis*) keep resin flowing about their nesting and roosting holes by pecking and tapping activities. This perhaps reduces predation by snakes and other enemies (Jackson 1978); possibly it may make it difficult for some competitors to usurp and use their holes, but this remains to be shown.

A final group of adaptations might be considered, namely social adaptations. Woodpeckers generally are aggressive birds (Blume 1968, Short 1974a), and this aggressiveness is displayed interspecifically (Short 1973, 1974b, 1975) as well as intraspecifically. Such aggression helps the woodpeckers to defend their nests, at least sometimes with success, against persistent potential usurpers (e.g., Starlings) incapable of excavating their own nests and against birds that may be of larger size (e.g., I have seen nesting *Picoides pubescens* drive away larger *P. villosus*, and *P. arcticus* keeps *Colaptes auratus* from proximity to its nest, Short 1974b). Despite intense aggression between competitors for nesting sites, such competitors at least occasionally appear "satisfied" once they have secured a nesting site, and there are many reports of nesting in proximity of usually aggressive nest-hole competitors with some, little or no aggression between them. Some examples are: (1) the nesting of *Picoides mahrattensis* and the parrot *Psittacula krameri* in the same tree with some attacks on the latter by the former (Eates 1937); (2) nesting of Northern Flickers and Pileated Woodpeckers on opposite sides of the same stub, the latter acting at times to drive the former away (Hoyt 1957); (3) the usurping of the nest of a pair of *Picoides syriacus* by *Passer montanus* and subsequent harmonious and successful nesting of *syriacus* in a newly excavated adjacent cavity that connected with that of the *Passer* (Szlivka 1960); (4) nesting in the same stub harmoniously of the usually interactive *Melanerpes chrysauchen* and *M. rubricapillus* (Skutch 1969); (5) nesting .6 m apart of *Melanerpes erythrocephalus* and *Colaptes auratus*, the former being dominant, with conflicts only when both species happened to visit the nest simultaneously (Reller 1972); and (6) nesting 1.4 m apart of *Melanerpes carolinus* and *Picoides borealis*, although the former usually is very aggressive to the latter (Jackson 1978).

Sociality itself is uncommon in picids, being mainly confined to terrestrial *Colaptes* and *Geocolaptes*, and to some melanerpine woodpeckers (Short 1970, 1971a, 1972, 1974c). These social picids are generalized in habits, and can concentrate in numbers because of their extensive simple habitat (open grasslands for *Colaptes, Geocolaptes*) or their omnivorous habits (especially melanerpine species). More "typical" woodpeckers that work the bark or wood for insect foods usually cannot concentrate in numbers, but must spread themselves through their habitat to insure sufficient foraging sites for individual and family needs. The social species have the advantage of numbers of adult individuals about the colony at all times (e.g., *Colaptes rupicola,* Short 1972; *Melanerpes striatus,* Short 1974c), available to protect the nesting bank or tree. The semi-social *Picoides borealis* shows this to come extent, but adults tend to feed and to visit the nest in groups, so adults are not present about the nest most of the time (Jackson, pers. comm.). In *Melanerpes cruentatus* (Short 1970) and *M. formicivorus* (MacRoberts and MacRoberts 1976) a number of adults beyond 1 pair are involved at a nest, and the nest is attended almost constantly. These habits doubtless afford greater protection to the nests than can be provided by a solitary pair of woodpeckers.

SUMMARY AND CONCLUSIONS

Woodpeckers excavate their own nesting cavities in hard or soft wood. Competitors for these cavities are numerous, and adversely affect the nesting efforts of many woodpeckers. Even other woodpeckers may usurp the partial or completed excavation of another woodpecker. However, picids show a number of adaptations that tend to reduce or minimize the loss of nests to competitors, such loss interfering as it does with the timing of nesting, and, when nesting sites are in short supply, with its success.

Losses that do occur are minimized by the ability of woodpeckers to renest rapidly, given suitable nesting sites. One factor in rapid renesting is the availability of other partly completed or completed holes (e.g., holes begun but discarded early in the nesting season, roosting holes) that can be used for renesting with minimum modification.

The avoidance of losses takes many forms, some of which are related as well to avoiding predation. Woodpeckers are closely associated with the nesting site from the time of excavation until the nestlings are active about the nest entrance, hence competitors are kept out of the cavity. There is little evidence for seasonal adjustment of breeding activities for temporal avoidance of competition with picid competitors, and no evidence regarding such adjustments to non-woodpecker competitors. Many woodpeckers use live wood in excavating their nest holes, and to the extent that they do so most competitors larger than the woodpecker are prevented from using the cavity because they are physically unable to alter (enlarge) it. Such holes often have deep tunnels from the entrance into the center of the tree, and the entrance itself usually is barely large enough to admit the woodpecker, hence large competitors must face difficulty not only in entering the cavity, but in sufficiently enlarging the tunnel, which usually penetrates hard wood. Picids, too, tend to choose as small a stub or tree as will permit construction of the nest, hence competitors of larger size will be unable to use the nest. Another tactic is to place the nest on the underside of a (small) branch, demanding great agility of potential competitors if they are to be successful. Some forest woodpeckers often choose a nesting tree outside the forest, precluding competition from arboreal mammals and reducing nest-site competition from hornbills and other secretive forest species. Human habitations outside the forest also are often the scene of woodpecker nesting efforts, again reducing competition from more secretive forest species, usually larger than the woodpecker, and sometimes hunted or otherwise persecuted by man. A few woodpeckers nest in ant or termite nests that are unsuitable for most nest-competitors. Social adaptations include the general aggressiveness of woodpeckers that aids them in retaining nests that are sought by competitors, and, in a few species, increased sociality that allows more individuals to defend the nest site or colony. These adaptations, when added to the basic capability of woodpeckers to excavate their own holes, several times in succession when forced to do so, account for the success woodpeckers have had in achieving a nearly cosmopolitan distribution in diverse habitats.

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SONG DIFFERENCES AND MAP DISTANCES IN A POPULATION OF ACADIAN FLYCATCHERS

Robert B. Payne and Paul Budde

Songs may vary among both local birds and local populations (Borror 1961, Borror and Gunn 1965). The variation among birds may allow birds to recognize each other as individuals. The variation among populations has sometimes been described in terms of "dialects," with neighboring birds having similar songs but populations no more than a few km away having quite distinct songs (Lemon 1966, 1975, Marler 1970, Harris and Lemon 1972, Baptista 1975, Mundinger 1975, Verner 1976). In a few species local geographic variation is less regular and may involve a few neighbors sharing similar songs, but other birds having no songs very similar to those of their neighbors (Borror and Gunn 1965), and a bird may share a song with only 1 neighbor (Thompson 1970, Kroodsma 1974). Few studies have sampled intensively a large proportion of the singing birds in a single locality and have described the microgeographic pattern of variation in song. The possible importance of song similarities in social behavior (Payne 1978), in the genetic differentiation of populations (Nottebohm 1969, Thielcke 1970), in adaptation of song to the physical features of the habitat (Nottebohm 1969), and in marking the structure and dispersal of bird populations (Baptista 1975) all make it desirable to investigate the variation in song on a local level. Here we describe individual variation and the microgeographic pattern of song similarity in a population of Acadian Flycatchers (*Empidonax virescens*). The population lives in a relatively homogeneous, linear habitat, the bottomland forest bordering the Potomac River in Montgomery County, Maryland. As the habitat is similar along the transect, the main effect separating the singing birds is simple linear distance.

The problem of relative similarities and differences in song structure among birds within local populations and between more remote assemblages of birds may be met usefully by applying multivariate statistical techniques. We compared measures of time and pitch in the songs of Acadian Flycatchers in relation to map distance. This avoids a subjective view of similarities as "dialects." We take the empirical approach that the associations of individuals in nature are unknown to us, but that we can recognize associations such as groups with similar songs by using the descriptive techniques of population phenetics (Sneath and Sokal 1973).

STUDY AREA AND METHODS

Acadian Flycatchers are common singing birds in the deciduous riverine forest along the Potomac River. Birds were recorded with a Uher 4000-L tape recorder and a Sennheiser MKH-805 directional microphone between 05:20 and 09:00 on the mornings of 1 and 2 July 1975. Map positions were determined for each bird from landmarks and mileage markers along the Chesapeake and Ohio Canal towpath, where the recordings were made. Birds were recorded in sequence, and birds on neighboring territories were distinguished by walking from the first to the second while both were singing.

Acadian Flycatchers give several rather simple vocalizations; the ones used in the comparisons here were the "advertising song," a territorial song transliterated as "*tee chup*" by Mumford (1964). We include the "dawn songs" recorded at the earliest times of 3 individuals (nos. 26, 27, 29), as this song ("*seet tee chup,*" or with additional introductory "seet" notes, as described by Mumford 1964) ends with the same pattern as the advertising song. Songs were analyzed with a Kay Elemetrics "Vibralyzer" 6030A at a wide band setting for maximal temporal resolution and a frequency range of 8 kHz. Audiospectrograms of 20 birds were sufficiently clear to allow measurement of frequency and time characters. The clearest song of each bird was chosen for measurement. In addition, audiospectrograms were produced for 10 consecutive songs of 1 bird to measure the variability of an individual.

For comparing the songs of flycatchers with each other, the measurements for each song were subjected to several univariate and multivariate analyses. In the multivariate analysis, correlation coefficients were computed for each pair of birds using the profile of data of 11 song characters for each bird, and phenetic distances for each pair were then computed as $D = 1 - r$, where r is the correlation coefficient of the pair. A phenogram was then derived from the resulting distance matrix to determine whether birds that are geographic neighbors tend to occur in clumps of similar songs. We determined x- and y- map coordinates for each bird from a map and then computed the map distance between every pair of birds. This distance is the shortest distance each bird would travel to visit each of the other flycatchers. As the curves of the river arc around some unsuitable unforested habitat, we also compared the phenetic song distances with the trail distances, where trail distances in miles were recorded directly from the C & O towpath markers and from local maps. In addition, the eigenvectors of standardized song characters were derived from a matrix of correlations in a principal component analysis, and the 2-dimensional PC ordination values were plotted for each bird to describe overall tendencies for neighboring birds to have similar songs. The multivariate techniques applied in the study have been used widely in numerical taxonomy and population phenetics and are discussed in Sneath and Sokal (1973), Cooley and Lohnes (1971), and Anderberg (1973).

RESULTS

Map locations of the 20 flycatchers are shown in Fig. 1. Birds were recorded mainly in 2 areas, from Edwards Ferry at mile marker 30.8 on the towpath, measured from the south end of the canal, downstream to mile 28.6, and from mile 17.5 just below Watts Branch downstream past Swains Lock to the Limekiln Branch above the Great Falls parking lot at mile 14.8. Elevation along the entire section is about 60 m above sea level,

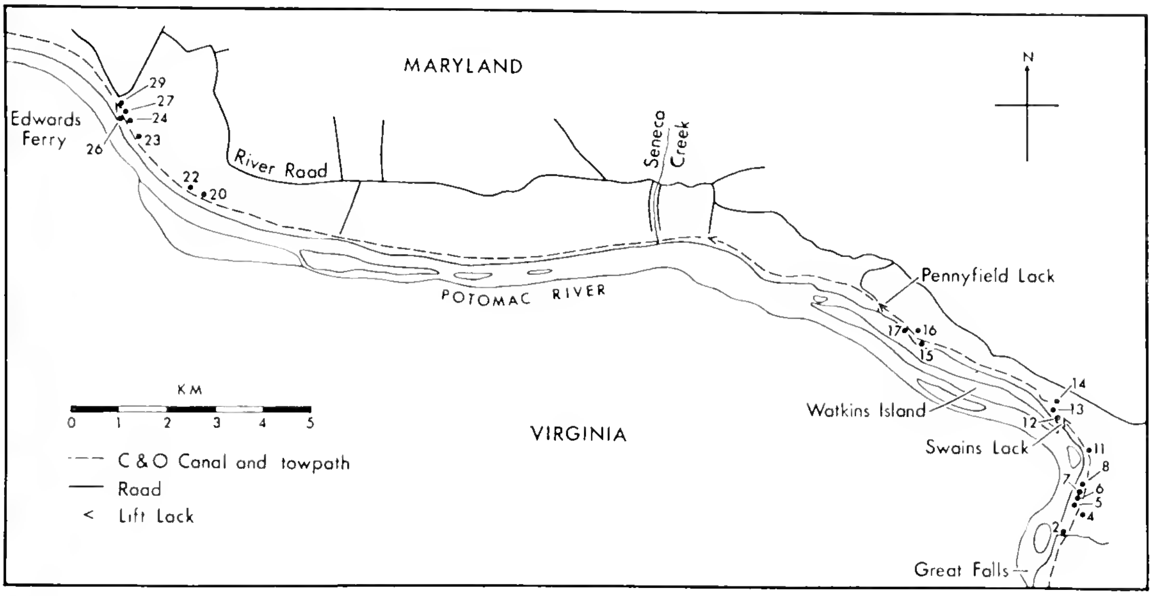

FIG. 1. Localities of Acadian Flycatchers recorded along the C & O Canal, Montgomery County, Maryland. Map after Clague 1963.

and the forest bordering the Maryland side of the river and both sides of the towpath is continuous in this section.

The song characters used in analysis included (1) frequency inflections on calibrated audiospectrograms and (2) temporal intervals. The beginning and end of notes rapidly rising or dropping in pitch were often unclear, and these notes seemed to start and end at a wide variety of frequencies. Marler and Isaac (1960) noted this result in another species and attributed it to differences in loudness as a function of distance. To avoid measurement error due to loudness, the temporal intervals of flycatcher song were measured at points along the intersection of the audiospectrogram figures and the 4 kHz calibration. The points of inflection where pitch could be measured with confidence (characters 1–6) and the temporal characters (7–11) are illustrated in Fig. 2, with representative songs of Acadian Flycatchers.

All song characters were variable in the population (Table 1). The temporal characters appeared to be more variable among birds than did the pitch characters, as the coefficients of variation (CV = SD/mean) are generally higher for the temporal characters (Table 1). Variation in a single bird's "*tee chup*" also is evident for all song characters (Table 2). Note that the CVs are uniformly lower for all 11 song characters of a single individual (bird 14) than for the sample of songs from 20 different birds. The calculated variance within this 1 bird was significantly less than the variance among the local birds ($F \geqslant 4.67$, $P < 0.05$) for 8 of the 11 song characters (exceptions were characters 3, 4, and 6). Data from 5 songs of

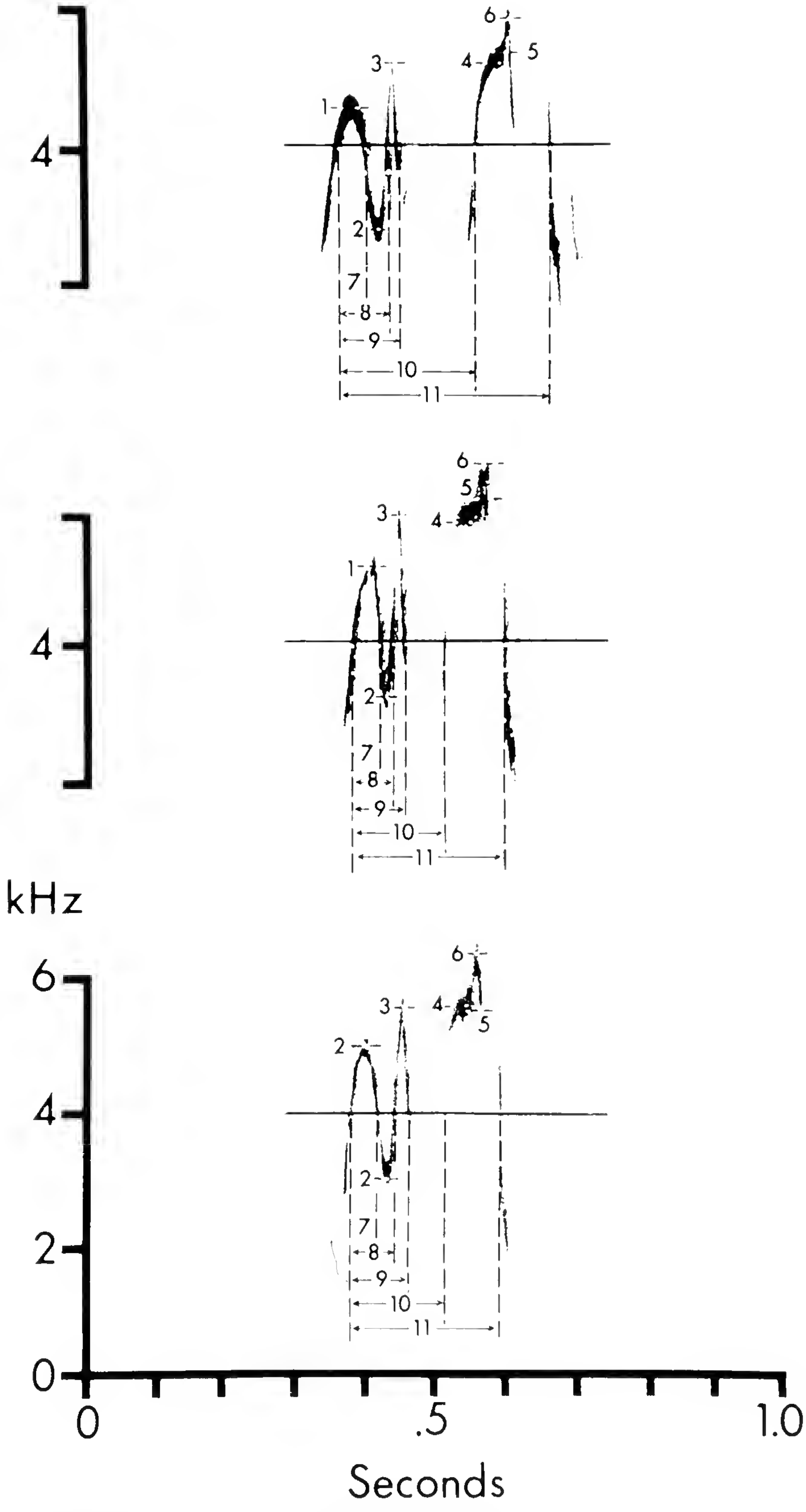

FIG. 2. Audiospectrograms of songs of 3 Acadian Flycatchers (nos. 14, 15, and 16) illustrating the 11 song characters measured.

TABLE 1

VARIATION IN 11 SONG CHARACTERS IN A POPULATION OF ACADIAN FLYCATCHERS

Variable and units	N	Min.	Max.	Mean	SD	CV
1 kHz	20	4.7	5.4	5.07	.208	.041
2 kHz	20	2.7	3.8	3.26	.373	.115
3 kHz	20	5.2	6.2	5.62	.278	.049
4 kHz	20	5.0	6.0	5.52	.271	.049
5 kHz	20	4.7	5.8	5.47	.270	.049
6 kHz	20	5.8	6.6	6.13	.231	.038
7 msec	20	90	150	116	17.5	.151
8 msec	20	125	205	165	24.5	.150
9 msec	20	165	260	214	22.5	.105
10 msec	20	320	560	387	69	.177
11 msec	20	550	830	638	92	.144

bird 7 and 6 songs of bird 5 also were examined and it appeared that the song characters were consistent within a bird in those smaller song samples as well. The results of Tables 1 and 2 suggest that the songs of an individual Acadian Flycatcher are less variable than are the songs of local flycatchers in general, and that much of the difference in song among individual flycatchers is in the temporal characteristics of the song. This appears to be the first quantitative study that shows individual song differences among the tyrannid flycatchers. Perhaps an observer or an Acadian Flycatcher

TABLE 2

VARIATION IN 11 SONG CHARACTERS IN 1 INDIVIDUAL ACADIAN FLYCATCHER

Variable and units	N	Min.	Max.	Mean	SD	CV
1 kHz	10	4.4	4.7	4.58	.103	.022
2 kHz	10	2.6	2.8	2.68	.063	.024
3 kHz	10	4.9	5.5	5.16	.190	.037
4 kHz	10	4.9	5.4	5.09	.152	.030
5 kHz	10	5.1	5.5	5.27	.125	.024
6 kHz	10	5.7	6.1	5.88	.140	.024
7 msec	10	100	125	116	8.3	.072
8 msec	10	190	210	197	6.3	.032
9 msec	10	220	250	236	8.3	.035
10 msec	10	495	575	531	22.9	.043
11 msec	10	755	860	805	28.8	.036

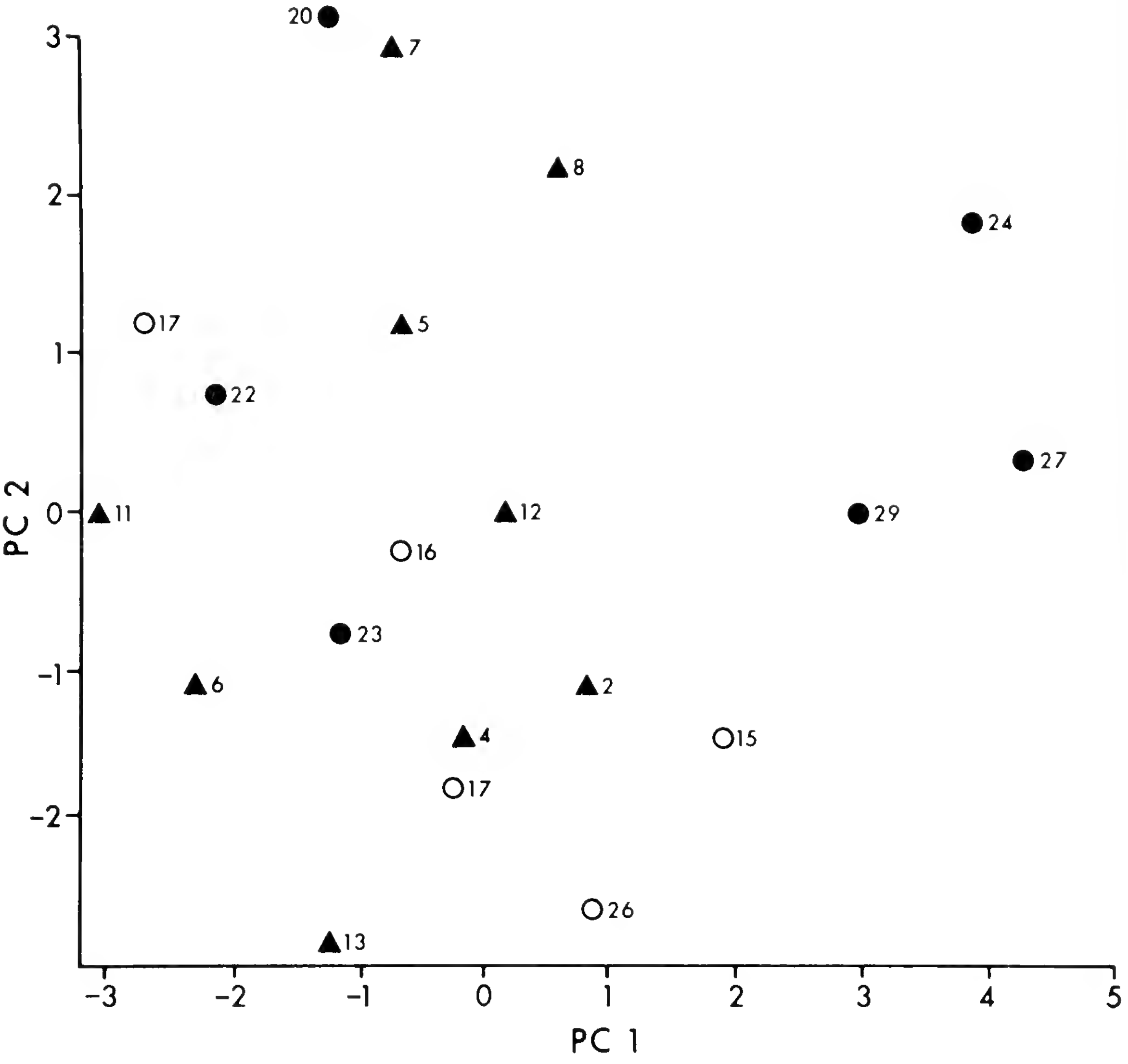

FIG. 3. Principal component analysis of the songs of 20 Acadian Flycatchers. Numbers refer to the individual birds shown in Fig. 1; triangles represent birds at the west end of the transect near Edwards Ferry, open circles are birds in the east-central part, and closed circles are birds at the east end near Great Falls.

could recognize a singing individual flycatcher, though the songs do sound similar.

We tested all the song characters to find whether any one was correlated with the map position of the bird along the towpath. No song character was significantly correlated with distance ($r_p \geqslant 0.39$, $P > 0.05$). Thus no song characters vary in a gradual way along the river in the area where we recorded the flycatchers.

A principal component analysis was completed for the 20 flycatchers to determine whether any natural clustering of birds from the ends of the transect was apparent. The results (Fig. 3) indicate no tendency for birds

TABLE 3

EIGENVECTORS OF 11 SONG CHARACTERS IN A PRINCIPAL COMPONENT ANALYSIS

Song character	Eigenvectors		
	PC 1	PC 2	PC 3
1	.358	.254	.209
2	.378	–.214	.028
3	.448	.096	–.044
4	.388	.142	.208
5	.311	–.149	.154
6	.376	–.096	.053
7	–.067	.485	.240
8	–.254	.466	.031
9	–.016	.546	.141
10	.118	.210	–.673
11	.236	.187	–.593
Component	4.29	2.98	1.68
Total cumulative variance	39.0%	66.1%	81.3%

to have distinct songs in the areas of Edwards Ferry, Swains Lock, and Great Falls. There is no tendency apparent for flycatcher song to form local "dialects" within distances of 4–8 km, nor is there a tendency for any dialect differentiation among birds 20 km apart. As with the individual song characters, the principal component results suggest no simple gradient in song variation along the river from Edwards Ferry to Great Falls. Analysis of the principal components results (Table 3) shows that the song characters with high eigenvalues on PC 1 are the pitch characters, those with high values on PC 2 are temporal characters 7–9, and those with high values on PC 3 are temporal characters 10 and 11. Hence even the clear interpretation of PC 1 as pitch and PC 2 as time does not allow a simple separation of flycatcher songs into local neighborhoods of similar song character combinations.

A phenogram or cluster tree derived from the matrix of correlation coefficients of standardized song characters and constructed using an unweighted averaging algorithm gives similar results (Fig. 4). Some neighboring birds were closely linked in the song phenogram, but this result was not general, nor were the birds for which we used the "dawn song" associated in a cluster, these instead were mixed among the other birds. This result is taken as justification for including these 3 birds in the analysis. Birds on adjacent territories show no strong tendency to have the most similar songs, and birds from the main areas along the river are not

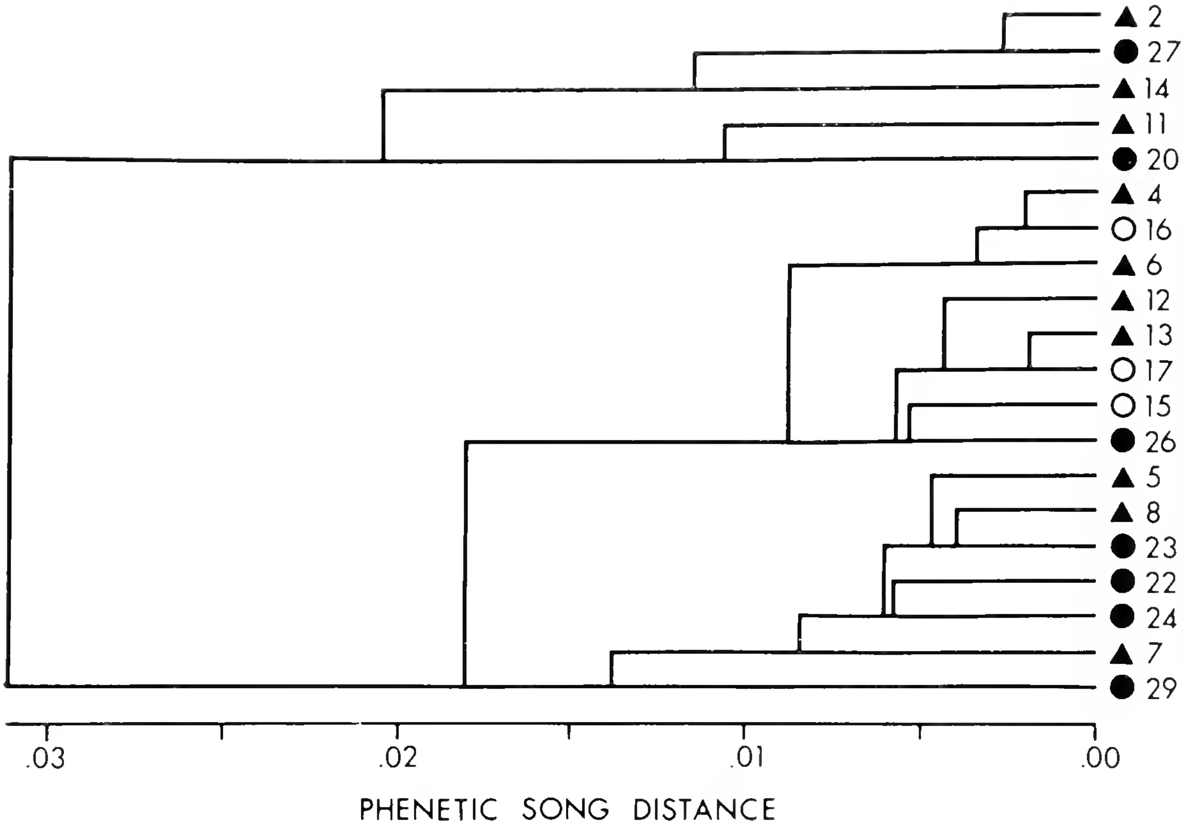

FIG. 4. Distance phenogram from a correlation matrix of 11 song characters of 20 Acadian Flycatchers clustered by unweighted pair-group averages of the standardized characters. The cophenetic correlation coefficient is .772.

closely associated in the figure. Although the cophenetic correlation coefficient is reasonably high (Sneath and Sokal 1973), a phenogram is a linear representation of a more complex distance matrix. The song phenetic distance values of the matrix were thus compared with the map distances of the territorial singing birds. If neighboring birds tended to have similar songs, whether song variation over a larger area were graded or were discontinuous as in a mosiac, one would expect to see a clustering of points in the lower left corner of the figure. As seen in the scatter diagram, there is no tendency for increasing song distance (or difference) with increasing map distance. There is no tendency for birds that are close neighbors, even birds on adjacent territories, to have songs more similar than birds at much greater distances. Substituting Euclidean map distances for the trail distances had little effect on the results. In Fig. 5 the intensity of points for low song phenetic distance (or, high song similarity) is about the same for birds near each other along the river as for those separated by several km, indicating that birds in a local neighborhood and within hearing distance of each other are no more similar in song than are those birds living farther apart.

To test whether birds on neighboring territories tended to have songs

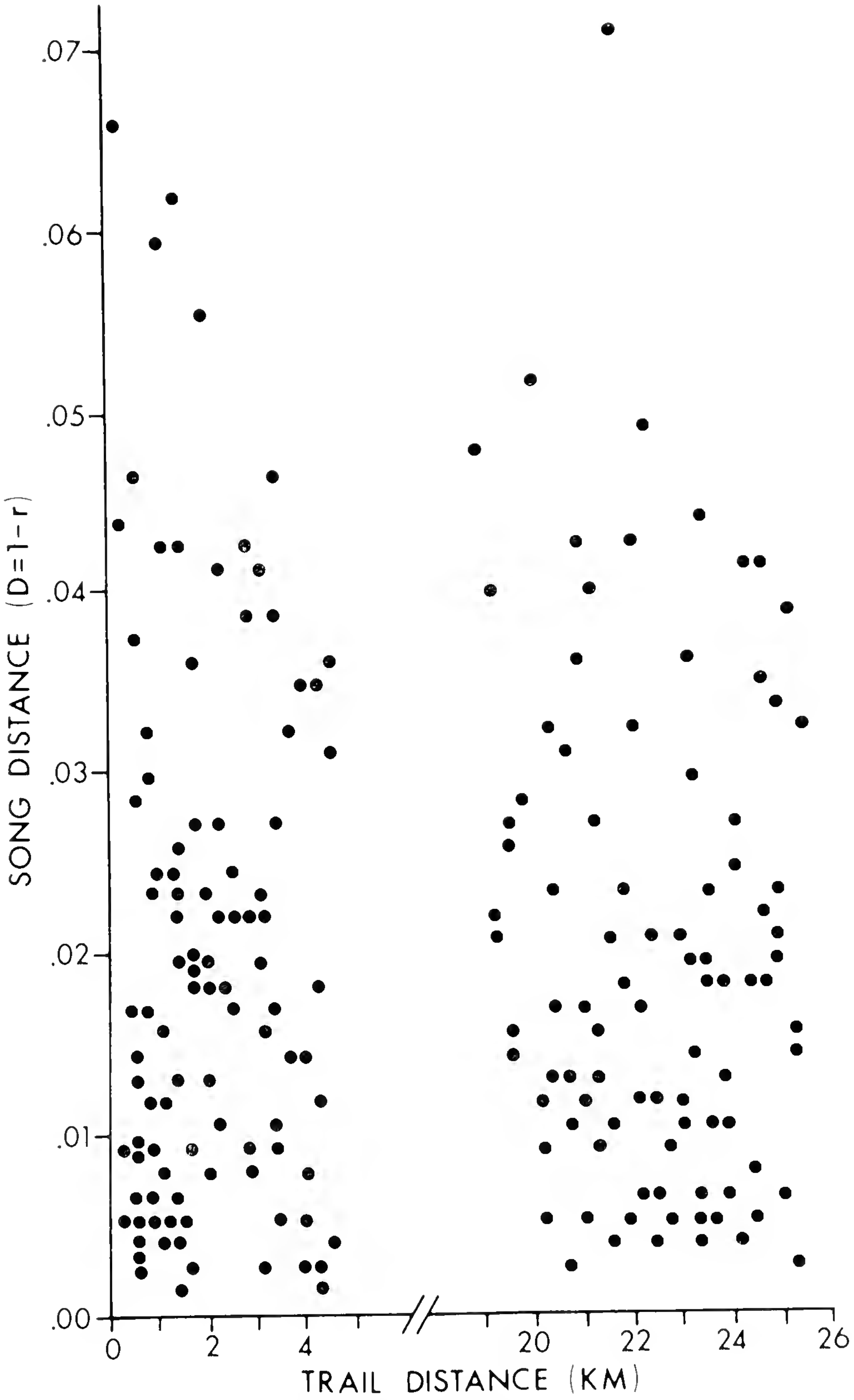

FIG. 5. Scatter diagram of microgeographic distances and phenetic song distances between Acadian Flycatchers. Note the lack of any tendency for the less remote birds to be more similar in their songs.

more similar to one another than birds not on neighboring territories, we compared the mean phenetic song distances of the 9 couplets of birds that were tape recorded within 100 m of each other with the 181 remaining phenetic song distances. Acadian Flycatchers have territories approximately 100 m across (Mumford 1964, Walkinshaw 1966), so birds recorded within 100 m are likely to be territorial neighbors, and in fact they were observed to be territorial neighbors in the field. The mean phenetic song distance of territorial neighbors was .0274. Analysis of the rank-order scores of the distances with a Mann-Whitney U-test ($U = 865$, $z = .314$, $P = .377$) shows that the mean phenetic distances in songs of adjacent and nonadjacent birds are not significantly different. Hence birds on adjacent territories do not have songs more similar to each other than to other birds in the local area.

DISCUSSION

Within the 30-km study area along the Potomac River, the Acadian Flycatchers show no evidence of local song dialects, song gradients with distance, or song similarities among birds on neighboring territories. A lack of behavioral differentiation in these local populations may be explained in several ways. First, some birds that have local dialects or have song sharing among neighbors and in which song development has been studied experimentally, are known to learn some features of their songs (Marler 1970, Rice and Thompson 1968, Dittus and Lemon 1969). Although local song variation does occur in some birds other than the songbirds (D. W. Snow 1968, B. Snow 1970, Mirsky 1976), it is unknown whether the pre-dispersal or post-dispersal songs heard by these birds affect the form of their songs. Perhaps the tyrannids such as the Acadian Flycatchers do not copy any particular song variant that they hear earlier in their lives.

Second, most birds with local dialects are nonmigratory but at least some birds disperse and then learn the songs of other adults in their new areas (Kroodsma 1974, Verner 1976). Acadian Flycatchers migrate to southern Central America and northern South America (A.O.U. Check-list, 1957). Adults usually return to the same locality in their breeding range year after year (Bird Banding Laboratory records). In Michigan, Walkinshaw (1966) found that nearly half of the banded, territorial Acadian Flycatchers returned to the same territory in successive years. Population structure in a genetic sense, however, is affected by the dispersal of young from the place of birth to the place of breeding in the adult years. Walkinshaw (1966) found no local returns for Acadian Flycatchers banded as young. The recoveries in the files of the Bird Banding Laboratory include only 2 birds ringed as a young in one year and recovered in a later year. One bird was recovered on 6 May in the year after hatching more than 160 km from the place of banding. The early date of recapture suggests that the bird may have been migrating, though the recapture was north of the site of banding. The second bird was recovered one BBL distance unit (a unit equals a block extending 0.1 degree on a side), and the recovery was within 16 km from the site of banding in the year after banding, suggesting a tendency to return to the area near the birthplace, though not to the same territory area of the parents. With only 2 banding recoveries, no general conclusions can be made about effective dispersal distance, but the lack of local returns in Walkinshaw's study suggests that Acadian Flycatchers usually do not return to the place of hatching, and that the distances of effective hatching-to-breeding dispersal are commonly greater than 1–2 km.

The function of the song in most dialectal birds or birds with song similarities among neighboring males includes territorial advertisement, as in the *Empidonax* flycatchers. Perhaps the individual differences in songs of the flycatchers are behaviorally significant in the recognition of neighboring individual males or in the recognition by females of the mates of earlier years or of the same year. Walkinshaw (1966) found that the same pairs formed in successive years, often on the same territories, even when the territory boundaries changed from year to year. However, we know of no experimental studies designed to test whether either the territorial males or their mates respond differently to the songs of different individual Acadian Flycatchers. The absence of song gradients with distance in our study area is consistent with the view that the birds all belong to a single effective population that extends across many social units of neighboring, territorial birds.

A similar analysis of phenetic song distance and microgeographic distance in another species, the Splendid Sunbird (*Nectarinia coccinigaster*), has shown a local similarity in song among neighbors where song and map distances are related only among birds that live closer than about 1 km (Payne 1978). This species is tropical and apparently nonmigratory. Quantitative analysis of song variation among other species of birds and its relation to the map distance among the birds may lead to a better understanding of the significance of local variations in the songs of birds.

SUMMARY

Tape recordings of the advertisement songs of 20 Acadian Flycatchers located within 30 km of each other along a continuous belt of lowland forest on the C & O Canal in Montgomery County, Maryland, were examined. Time and frequency measurements indicated that the songs of an individual are significantly less variable than the songs of different individuals. Songs were subjected to multivariate statistical analyses for detection of behavioral differentiation of local populations. No pattern of local song dialects or of song matching by neighboring territorial males was found in these flycatchers. Phenetic distances between songs were not related in any simple manner to the microgeographic map distances between the birds. The results are consistent with a pattern of effective dispersal of the young from their place of birth to their place of breeding and with a view of the birds as comprising a very large effective population. We suggest that multivariate phenetic analysis of bird songs may help provide a common basis for comparing patterns of geographic variation in bird songs.

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TIME BUDGET OF BREEDING NORTHERN SHOVELERS

ALAN D. AFTON

McKinney (1970) suggested that the plankton-straining habits of Northern Shovelers (*Anas clypeata*) might require them to spend proportionately more time foraging than many other dabbling ducks. McKinney (1973, 1975) further suggested that a time consuming feeding method would entail special problems for breeding females and thus would have favored the evolution of the Northern Shoveler territorial system. This paper describes time budgets of Northern Shoveler pairs during the breeding season. Results are discussed in relation to the importance of stored body reserves and environmental food resources to breeding females.

STUDY AREA AND METHODS

The study was conducted near the Delta Marsh in south central Manitoba, Canada. Observations of pairs were made in the aspen parklands adjoining the marsh. The area has been described by Conner (1939), Hochbaum (1944), Löve and Löve (1954), Sowls (1955), Ellis (1959), and Bird (1961).

Shovelers were captured with rocket nets, decoy traps (Blohm and Ward 1979), or nest traps (Weller 1957), and individually marked with nasal saddles (Sugden and Poston 1968). Some unmarked individuals were identified by variations of plumage and bill edge coloration. Observations were made with binoculars (7×) or a telescope (20–45×) from a truck and recorded with a portable tape recorder.

Time budgets of pairs were calculated during spring arrival, prelaying, and laying in 1975 by procedures similar to those of Dwyer (1975). Activities of pair members were continuously recorded during 1 h sampling periods randomly selected from 3 periods of the day, 05:00–10:00, 10:00–15:00, and 15:00–20:00. Activities were separated into 7 categories: (1) feeding; (2) resting (loafing and sleeping); (3) comfort movements; (4) locomotion (walking, swimming, and flying not associated with aerial pursuits); (5) alert; (6) social interactions (threats, chasing, pursuit flights, and inciting); and (7) out of sight. Calculations of the percent of time spent in various activities were based on the amount of time individuals were actually observed. Time budgets of incubating females were determined during recesses (periods off the nest). I observed marked females at known incubation stages by waiting for the hen to leave the nest and then continuously recording her behavior until she returned. Only complete, undisturbed sampling periods and recesses were analyzed. Sexual differences in activities within breeding stages were determined by paired t tests.

RESULTS

Spring arrival.—Upon arrival on the breeding grounds in mid April, flocks of pairs occupied shallow depressions in stubble fields and flooded meadows adjacent to the marsh. Paired males were generally non-aggressive upon arrival, and pairs often fed or rested within 1 m of each

TABLE 1

PERCENT OF TIME SPENT IN VARIOUS ACTIVITIES BY NORTHERN SHOVELER PAIRS DURING SPRING ARRIVAL (N = 12 H), PRELAYING (N = 18 H), AND LAYING (N = 13 H), AND BY FEMALES DURING 11 INCUBATION RECESSES

Breeding stage	Percent of time spent: Feeding	Resting	Comfort movements	Locomotion	Alert	Social interactions
Spring arrival						
males	63.5	18.5	6.3	3.0	7.4	1.3
females	68.9	16.1	10.3	1.8	2.6	0.3
Prelaying						
males	54.2	21.6	12.1	5.8	4.8	1.5
females	58.4	24.1	11.4	3.1	2.8	0.2
Laying						
males	34.9	14.7	19.0	6.8	24.3	0.3
females	57.1	18.6	17.9	2.0	4.3	0.1
Incubation						
females	68.3	1.1	23.3	4.6	2.6	0.1

other. Hostility increased after unpaired males arrived, and paired males began defending an area of 1 to 3 m radius around their mobile females (Seymour 1974, Afton 1977).

Pairs spent most of the daylight hours feeding or resting during spring arrival (Table 1). Females devoted more time to comfort movements ($P < 0.01$), while males spent more time in social interactions ($P < 0.02$). Pair members spent similar amounts of time feeding, resting, alert, and in locomotion ($P > 0.05$).

Prelaying.—Within 1 to 2 weeks after arrival, pairs dispersed from flocks and established breeding territories (Seymour 1974). All observations during prelaying were of territorial pairs. Territories were defended for a minimum of 10 to 18 days prior to laying ($\bar{x} = 14.2$, SE = 1.5, N = 5).

Daily activities of 4 pairs consisted primarily of feeding and resting during prelaying (Table 1). Foraging rates of females were significantly greater than those of their mates ($P < 0.02$). Males spent more time than females in locomotion ($P < 0.02$), alert behavior ($P < 0.02$), and social interactions ($P < 0.02$). Pair members devoted similar amounts of time to comfort movements and resting ($P > 0.05$).

Laying.—Females spent increasing amounts of time on the nest as laying progressed. The relationship was best described by the equation Y =

$0.027 + 0.585X^2$ ($F = 108.237$, $P < 0.001$, $r^2 = 0.857$), where Y = proportion of day spent on the nest, and X = proportion of clutch completed (Afton 1977). Thus, a hen with a 10 egg clutch spent, on the average, 74.8% of her time during the laying stage off the nest.

Table 1 shows daily activities of 5 pairs when females were off their nests during the laying stage. Females spent significantly more time feeding than did males ($P < 0.001$). Correspondingly, males spent more time alert ($P < 0.001$) and in locomotion ($P < 0.01$) than females. Comfort movements, resting, and social interactions consumed similar amounts of time for pair members ($P > 0.05$).

Seasonal trends in activities.—General trends are evident in the daily activities of pairs during the breeding season (Table 1). Foraging rates declined for both sexes as the season progressed, but the decline was much greater for males (28.6% vs. 11.8%). Females fed more intensively than their mates in all 3 breeding stages. Continuous foraging bouts of hens averaged 3.5 min (SE = 0.5, N = 113), 3.6 min (SE = 0.4, N = 129), and 4.4 min (SE = 0.7, N = 76) during spring arrival, prelaying, and laying, respectively; those of drakes averaged 1.9 min (SE = 0.2, N = 195), 1.9 min (SE = 0.2, N = 228), and 1.2 min (SE = 0.1, N = 193). Feeding occurred during all daylight hours, while resting increased during midday in all breeding stages. During prelaying and laying, females typically fed while their mates were involved in social interactions with conspecifics. Comfort activities increased for both sexes during the season. Males spent considerably more time alert during laying than in the previous stages.

Incubation recesses.—During the 23 day incubation period, females spent an average of 221.3 min (SE = 6.9, N = 120) off the nest each day (Afton 1977). Recess activities of 6 hens consisted mainly of feeding and comfort movements (Table 1). The proportion of time spent feeding during recesses increased throughout incubation, while time spent in comfort movements and locomotion decreased (Fig. 1). Other activities showed no significant relationship to stage of incubation. The paired male was usually present on the territory and immediately swam or flew to his mate when she arrived from the nest. He remained alert and in constant attendance for the duration of the recess.

DISCUSSION

Sexual differences in foraging rates apparently reflect differential energetic costs of reproduction. The caloric cost of egg production is relatively high for anseriforms (King 1973, Ricklefs 1974), and breeding ducks require

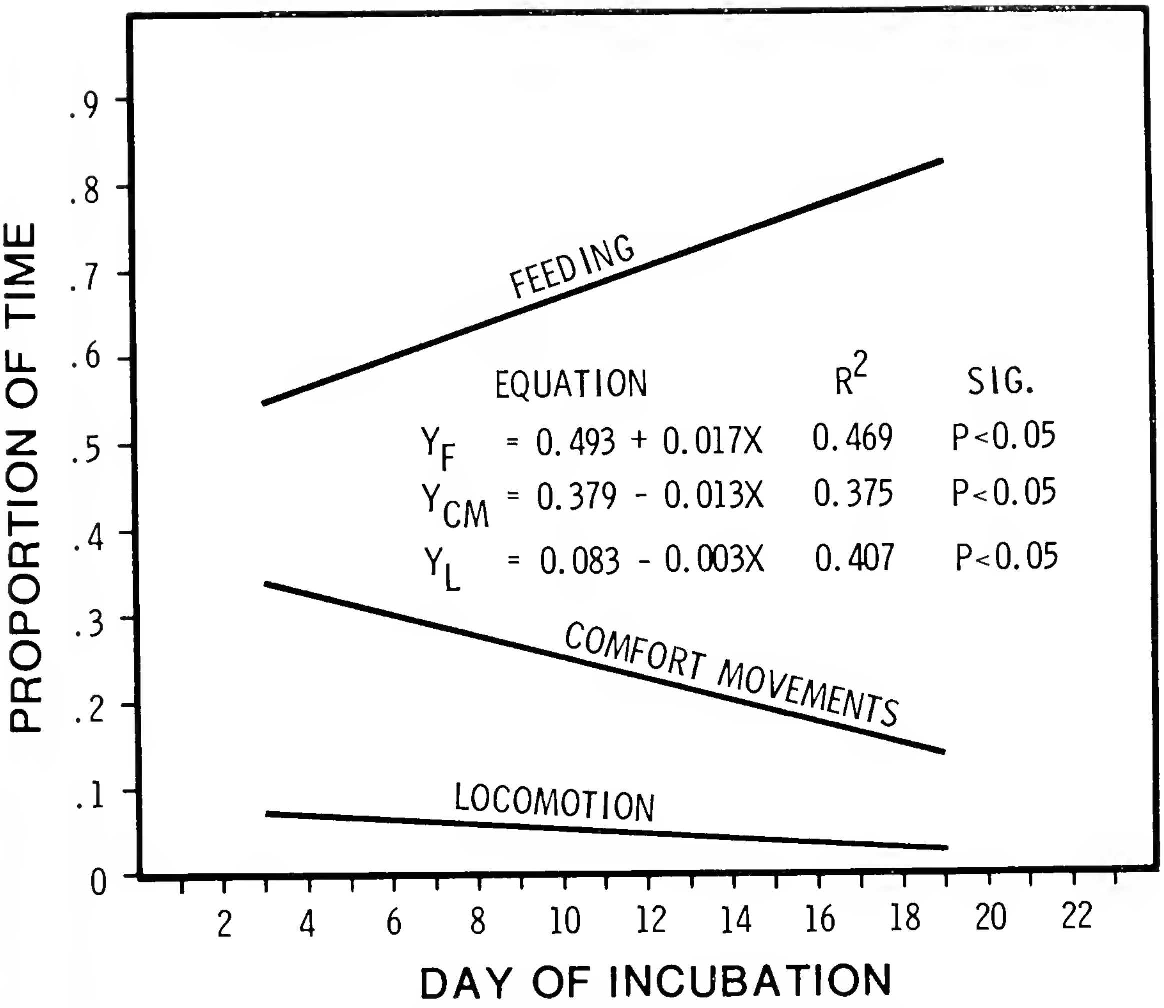

FIG. 1. Relationship of the proportion of time spent feeding, in comfort movements, and in locomotion during incubation recesses ($N = 11$) to stage of incubation, for 6 female Northern Shovelers.

large amounts of protein in the form of aquatic invertebrates (Holm and Scott 1954, Krapu and Swanson 1975). Similar sexual differences in foraging rates have been reported for other anatids during the breeding season (Bengtson 1972, Titman 1973, Dwyer 1974, 1975, Milne 1974, Swanson et al. 1974, Ashcroft 1976, Derrickson 1977, Stewart 1977, Seymour and Titman 1978).

My data do not support McKinney's (1970) hypothesis that the Northern Shoveler's feeding method is relatively more time consuming when compared to time budget data for other *Anas* species (Titman 1973, Dwyer 1975, Miller 1976, Derrickson 1977, Stewart 1977, Seymour and Titman 1978). Additional studies on time and energy expenditures of breeding ducks are clearly needed. However, interspecific comparisons of feeding rates must be made with caution as species differ in body size, foraging methods, diets, and possibly in the amount of time spent feeding at night.

Northern Shoveler hens apparently rely primarily upon breeding ground food resources for reproduction. Upon arrival on the breeding grounds, hens spend approximately 3 weeks mostly feeding and accumulate endogenous reserves (Afton in prep.) that are used during laying and incubation. In contrast arctic nesting geese and possibly early nesting dabbling ducks (e.g., Pintails, *Anas acuta*) rely almost exclusively on endogenous reserves acquired prior to arrival on the breeding grounds (Ryder 1970, Krapu 1974, MacInnes et al. 1974, Ankney 1977, Ankney and MacInnes 1978).

Shoveler hens support their metabolism during incubation through periodic foraging and by relying heavily on stored body reserves (Afton in prep.). However, I believe environmental food resources are critical to successful incubation because: (1) females foraged most of their time off the nest; (2) the proportion of time spent feeding during recesses increased throughout incubation; (3) shovelers were correspondingly less attentive to their nests than larger anatids (Afton 1977); (4) gizzards of female shovelers did not decrease in size during incubation (Afton in prep.), unlike those of Common Eiders (*Somateria mollissima*) (Cantin et al. 1974, Milne 1976) and Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney 1977) which feed little during incubation; (5) paired males maintained territories, on the average, until day 21 of incubation, the same day on which females markedly increased nest attentiveness (Afton 1977); and (6) 1 marked hen, whose mate was killed in early incubation, deserted her nest 4 days after another pair established on the same territory. Harassment by the new paired drake prevented the marked hen from feeding during recesses. Thus, I believe the desertion resulted from insufficient foraging time.

The apparent crucial importance of environmental food resources to shoveler hens during incubation contrasts the situation found in geese (Ryder 1970, Harvey 1971, Cooper 1978, MacInnes et al. 1974, Ankney 1977, Ankney and MacInnes 1978) and Common Eiders (Milne 1974, 1976, Korschgen 1977) which rely almost exclusively on stored body reserves. These larger anatids maintain high nest attentiveness which is adaptive in reducing the exposure of eggs to weather and predation. Due to their relatively small body size, shoveler hens probably are unable to store sufficiently large amounts of body reserves to carry them through incubation, and therefore, must rely heavily on environmental food resources. Available data support the hypothesis that small female anatids rely to a greater extent on food resources during incubation (Table 2).

Shoveler males maintained isolation for their mates through territorial defense. Consequently, foraging bouts of hens were rarely interrupted after territory establishment. The successive decline in male feeding rates partially resulted from increased time spent alert and swimming with head

TABLE 2

ESTIMATED FEEDING TIME DURING INCUBATION FOR 4 ANATIDS

Species	Incubation period (days)	Mean time off nest/day (min)	Proportion of time spent feeding	Feeding time/day (min)	Total feeding time (h)
Branta canadensis[a]	27	20.2	0.377	7.6	3.4
Anas platyrhynchos[b, c]	26	78.0	0.674	52.6	22.8
Anas clypeata[d]	23	221.3	0.683	151.1	57.9
Anas discors[e]	23	289.0	0.600	173.4	66.5

References: [a] Cooper (1978), [b] Caldwell and Cornwell (1975), [c] Titman (1973), [d] Afton (1977), [e] Miller (1976).

upright. Both activities were important for successful territorial defense and probably also had predator escape functions. Drakes were probably able to reduce foraging time because of increasing food resources due to higher air temperatures and longer photoperiods (Dwyer 1975) and/or perhaps by relying partially on stored body reserves.

In general, my data support the contentions of McKinney (1973, 1975) and Seymour (1974) that defense of a territory is advantageous in securing a needed food supply for the hen and providing her with undisturbed feeding time. Since the hen's reproductive success is critically dependent on breeding ground food resources, the male's fidelity to his mate and persistent defense of a feeding territory is necessary to assure his own reproductive success. Thus, I believe that the female's strategy in obtaining energy for reproduction has been an important factor in the evolution of the Northern Shoveler breeding system.

SUMMARY

Behavior of Northern Shoveler pairs was studied during the 1975 breeding season near Delta, Manitoba. Time budget analysis indicated that paired females spent approximately 3 weeks, mostly feeding, on the breeding grounds prior to laying. Sexual differences in foraging rates were detected, and apparently reflect differential energetic costs of reproduction. Paired males maintained isolation for their mates through territorial defense. Consequently, foraging bouts of hens were rarely interrupted after territory establishment. Environmental food resources were apparently critically important for successful incubation. The female's strategy in obtaining energy for reproduction may have been an important factor in the evolution of the Northern Shoveler breeding system.

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THE BIOLOGY AND NESTING DENSITY OF BREEDING AMERICAN KESTRELS AND LONG-EARED OWLS ON THE BIG LOST RIVER, SOUTHEASTERN IDAHO

Timothy H. Craig and Charles H. Trost

This study addresses some nesting parameters of American Kestrels (*Falco sparverius*) and Long-eared Owls (*Asio otus*) along the Big Lost River on the Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho. Although both are common raptors over much of North America, little attention has been paid to the nesting parameters of either in a desert environment, and no reports on North American Long-eared Owls have considered as many nests through a breeding season as the present study.

STUDY AREA AND METHODS

The INEL Site is a 2315 km^2 government reservation on the upper Snake River Plain. The area is a cool desert (Odum 1971) and big sagebrush (*Artemisia tridentata*)-grass vegetation types are predominant (Harniss and West 1973). The average elevation of the INEL Site is 1524 m and the topography is flat to rolling.

The study was conducted along 25 km of the Big Lost River which flows into the INEL Site before disappearing into the Big Lost River Sinks near Howe, Idaho. The river flows for much of the spring and early summer; but by late summer the flow on the lower river has been greatly reduced or eliminated by the diminished snow melt and the upstream removal of irrigation water. The average width of the upper reaches of the Big Lost River on the INEL Site is 9.6 m (Kerry Overton, pers. comm.). The characteristic vegetation of the Snake River Plain is interrupted along the Big Lost River by cottonwood trees (*Populus* spp.) which grow immediately along its banks. These trees range in size from saplings to well over 9 m tall and they occur sporadically along the lower part of the river.

Our observations on the INEL Site took place in 1975 and 1976. The spring of 1975 was cool and wet, while the spring of 1976 was comparatively warm and dry. In the nesting season (March through August) the average precipitation was 12.6 cm in 1976 and 14.7 cm in 1975 and the average temperature was nearly 2°C lower in 1975 than in 1976. In particular, the months of April and May averaged 4.5°C and 5.8°C cooler in 1975 than 1976 and the average precipitation was 0.3 cm and 0.2 cm greater for those months in 1975 than 1976 (National Oceanographic and Atmospheric Administration records).

In 1975, 7 nesting boxes (see Hammerstrom et al. 1973) were placed 3 to 8 m high in cottonwood trees along the upper 8 km of the Big Lost River on the study area. In 1976, 7 more nesting boxes were placed along the same section of river and 6 were placed further downstream. The boxes were widely separated along the river.

In late March of 1975 and early April of 1976, TC surveyed the Big Lost River by walking the river bank and investigating each tree which contained a large nest or cavity. The study area was surveyed again in May and June both years to be sure any late-nesting birds were found.

To avoid disturbing the birds, a nest was not visited until it was decided that the eggs probably had hatched. Because nesting dates varied considerably, some nests were visited twice during incubation while others were not revisited until the young were 7 to 10 days old.

After most nests had young in them, TC checked each every 2 days in 1975 and 3 days in 1976 and removed all prey remains that were no longer of food value to the young. Castings were removed only from Long-eared Owl nests since the bony remains in them are easily identifiable (Errington 1930) and hawk castings offer little reliable food habit data (Errington 1932). The material in the castings was identified by comparison with skeletons from the Idaho State University Museum collection.

The number of eggs or young in nests was determined by direct observation. In nests that were not visited until after all young had hatched, we assumed that any unhatched egg would be left in the nest for a short period of time; therefore, clutch-size and brood-size were considered the same if the nests were visited no later than 4 days after the youngest nestling had hatched. Three Long-eared Owl nests were found in 1975, 2 after the young fledged; thus, the number of eggs laid per nest was determined by the number of young seen in the 2 family groups plus the contents of 1 other nest.

Only nests in which eggs were laid were considered in calculating productivity. The number of young American Kestrels fledged from a nest was determined by counting the number of young which were still in the nest no more than 3 days prior to the time it was vacated. Since Long-eared Owls move out of the nest onto branches in the nest tree and nearby trees before they are free-flying (Whitman 1924), we assumed that they had fledged if they were seen at or around the nest or in branches of the nest tree.

The percent biomass of prey items in the diet of these raptors was calculated using individual mass values obtained from Kochert (1975), Poole (1938), Spector (1956), Tinkle (1973) or from mean weights of specimens in the Idaho State University Museum.

RESULTS AND DISCUSSION

American Kestrel Nesting Biology

Phenology.—American Kestrels were not resident on the INEL Site but arrived in late March and April. Using an incubation period of 30 days (Roest 1957, Smith et al. 1972) we calculated that the first American Kestrels to nest on the Site began incubating eggs in mid-May in 1975 and 12 days earlier (early May) in 1976 (Fig. 1). The mean hatching and fledging dates for 10 nests in 1975 were 25 June and 24 July, respectively. In 1976 the mean hatching date for 14 nests was 12 June and the mean fledging date was 9 July. The onset of nesting behavior was varied and in both 1975 and 1976 more than 3 weeks elapsed between the earliest egg hatching dates and the latest.

Young American Kestrels hatched 12 days earlier in 1976 than in 1975 and there was a 13-day difference in the mean egg hatching dates. The mean fledging dates were even more variable and occurred 15 days later in 1975. The cooler, wetter spring, particularly during courtship and egg-laying (April and May) may have delayed the onset of nesting in 1975. Roest

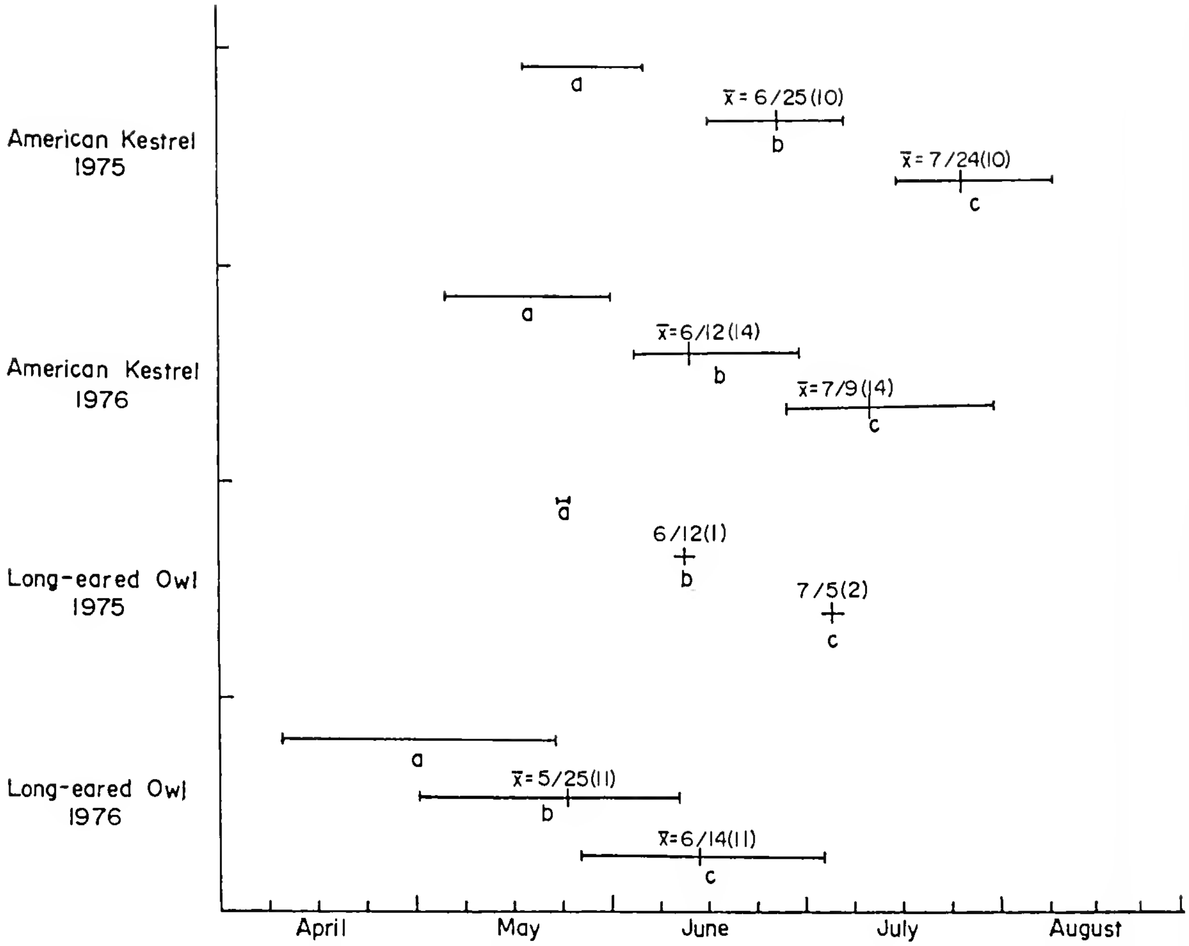

FIG. 1. Nesting phenology (bar represents length of time from earliest to latest dates) of American Kestrels and Long-eared Owls on the INEL Site in 1975 and 1976, showing mean dates and sample sizes; a = egg-laying, b = hatching, c = fledging.

(1957) suggests that egg-laying dates for American Kestrels are probably dependent upon local weather conditions. An increase in available prey in the early spring might also have hastened the onset of nesting behavior, though we collected no data on prey availability.

The period of time from hatching to fledging, 29.3 ± 3.9 (SD) days in 1975 versus 27.7 ± 3.5 days in 1976, is not significantly different in the 2 years (Group Comparison *t*; $t = 1.04$, $P > 0.05$). Porter and Wiemeyer (1972) reported that captive American Kestrels were in the nest an average of 28.4 days (26–32 day range), while Craighead and Craighead (1956) reported 31 and 29 days for wild birds in Michigan and Wyoming, respectively.

Productivity.—The mean number of eggs in American Kestrel nests in 1975 was 4.5 ± 0.7 and 4.7 ± 0.7 in 1976 (Table 1). In 1975 a mean of 3.7 ± 1.8 young hatched from these nests and in 1976 the mean was 4.0 ± 1.8 young/nest. In both years all young which hatched also fledged

TABLE 1

MEAN CLUTCH-SIZE AND NESTING PRODUCTIVITY OF AMERICAN KESTRELS AND LONG-EARED OWLS ON THE INEL SITE IN 1975 AND 1976

	N	Mean clutch-size	Percent of nests hatching							Mean
			0 eggs	1 eggs	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	
American Kestrel 1975	13	4.5	15.4	0.0	7.7	0.0	30.8	46.1	0.0	3.7
American Kestrel 1976	23	4.7	13.0	4.4	0.0	0.0	21.7	60.9	0.0	4.0
Long-eared Owl 1975	3	3.0	0.0	0.0	66.7	33.3	0.0	0.0	0.0	2.3
Long-eared Owl 1976	15	5.3	13.3	0.0	6.7	0.0	6.7	60.0	13.3	4.2

	N	Percent of nests fledging							Mean
		0 young	1 young	2 young	3 young	4 young	5 young	6 young	
American Kestrel 1975	13	15.4	0.0	7.7	0.0	30.8	46.1	0.0	3.7
American Kestrel 1976	23	13.0	4.4	0.0	0.0	21.7	60.9	0.0	4.0
Long-eared Owl 1975	3	33.3	0.0	33.3	33.3	0.0	0.0	0.0	1.7
Long-eared Owl 1976	16	12.5	0.0	6.2	0.0	25.0	43.8	12.5	4.1

successfully. There were no significant differences in the productivity ($\bar{x}$ number of young to fledge) of American Kestrels in 1975 and 1976 (Group Comparison *t*; $t = .42$, $P > 0.05$). More nests fledged 5 young than any other number and there was a higher percent of nests to contain 5 eggs and fledge 5 young in 1976 than in 1975 (60.9% vs. 46.2%). Smith et al. (1972) also found that the most frequently occurring clutch-size was 5 eggs. Although other researchers report up to 6 eggs (Bent 1938, Roest 1957, Smith et al. 1972), none of the nests on the INEL Site contained more than 5 eggs. The mean productivity of American Kestrels on the INEL Site approximated that reported by Hamerstrom et al. (1973) of 4.0 young/nest and Nagy (1963) of 4.4 young/nest; N = 7. However, it was higher than that reported by Smith et al. in 1972 (2.3 young/nest: N = 22), in Utah. Since young American Kestrels were assumed to have fledged if they were seen in the nest 3 days prior to the time the nest was vacated, the actual mean number of young to fledge from nests would be expected to be somewhat lower than reported herein.

There was an 80% increase in the number of active American Kestrel nests that were found from 1975 to 1976 (from 13 nests or 0.5 nests/km of river to 23 nests or 0.9 nests/km of river). This increase may have resulted from the improved weather conditions in 1976 or because 13 more nest boxes were placed on the study area in 1976.

Nest boxes.—Of the 7 nest boxes available in 1975, 3 were successfully used by American Kestrels. Two others were visited by American Kestrels early in the year but as the sides were removed no nesting occurred. Two others were used by Starlings (*Sturnus vulgaris*) and Common Flickers (*Colaptes auratus*).

American Kestrels visited 11 nests boxes in 1976 and successfully hatched eggs in all but 2, where the clutches failed. Eight other nest boxes were used by Starlings; 1 box was not used. In 1 successful nest box, we found 2 Starling eggs with a clutch of 5 American Kestrel eggs.

Since we found only 30 potential natural nesting cavities along the Big Lost River (many were used by other bird species) the nest boxes may have influenced the number of nesting pairs of American Kestrels on the study area. They did not affect productivity as there was no significant difference in the productivity of American Kestrels in nest boxes and in natural nest sites (Group Comparison t; $t = .04$, $P > 0.05$).

Nest-sites.—The average entrance diameter of 12 American Kestrel nests along the Big Lost River was 9.3 ± 3.5 cm (range, 7.5 cm–18.0 cm) and the average height of 17 nests was 2.7 ± 1.4 m (range, 1.0 m–6.0 m). Three of the nests were in snags, the tops of which were completely open. Two American Kestrel nests were in old Black-billed Magpie (*Pica pica*) nests which had intact canopies similar to those reported by Roest (1957) and Bent (1938). One of these nests was in the same tree in which a Long-eared Owl nested. Another American Kestrel nest, in a nest box, was in the same tree in which a Red-tailed Hawk (*Buteo jamaicensis*) nested. Some American Kestrel nests were as close together as 100 m. Nagy (1963) reported nests which were 33 m apart. Eight of the American Kestrel nests used in 1975 were reused in 1976 (3 were in nest boxes). Both Craighead and Craighead (1956) and Smith et al. (1972) found that some American Kestrel nests were reused on their study areas.

Food habits.—In 1975 and 1976, the majority of the diet by biomass of the American Kestrel was avian prey (Table 2). Most were unidentified passerines or Western Meadowlarks (*Sturnella neglecta*) which were presumably captured as young birds since Western Meadowlarks fledge in the first weeks of June (Timothy Reynolds, pers. comm.). Conversely, Smith et al. (1972) and Heintzelman (1964) found more mammalian remains than avian remains in American Kestrel nests. In 1976, the percent biomass of mammals increased from 15.7 to 44.9% while the reptilian component dropped from 15.8 to 1.5%. The reason for this shift in prey remains may be the timing of nesting on the INEL Site. In 1975 American Kestrels were feeding their young later in the summer, when reptiles and young passerines were more available. Smith et al. (1972) found 3.0% of the total prey biomass to be

TABLE 2

PREY REMAINS FOUND IN AMERICAN KESTREL NESTS ON THE INEL SITE IN 1975 AND 1976

	1975 (9 nests)			1976 (10 nests)		
	N	Biomass (g)	% biomass	N	Biomass (g)	% biomass
Ord's kangaroo rat (*Dipodomys ordii*)	0	0.0	0.0	1	55.5	1.8
Deer mouse (*Peromyscus maniculatus*)	3	51.0	2.8	2	34.0	1.1
Montane vole (*Microtus montanus*)	0	0.0	0.0	7	241.5	7.6
Least chipmunk (*Eutamius minimus*)	3	234.0	12.9	13	1014.0	32.0
Northern pocket gopher (*Thomomys talpoides*)	0	0.0	0.0	1	76.0	2.4
Starling (*Sturnus vulgaris*)	0	0.0	0.0	3	180.0	5.7
Western Meadowlark (*Sturnella neglecta*)	8	768.0	42.4	12	1152.0	36.3
Common Flicker (*Colaptes auratus*)	1	100.0	5.5	0	0.0	0.0
Unidentified birds	15	360.0	19.9	15	360.0	11.4
Short-horned lizard (*Phrynosoma douglassi*)	11	267.3	14.8	1	24.3	0.8
Sagebrush lizard (*Sceloporus graciosus*)	6	18.0	1.0	7	21.0	0.7
Insects	12	12.6	0.7	11	6.6	0.2
Total	59	1810.9	100.0	73	3164.9	100.0
% Mammal			15.7			44.9
% Bird			67.8			53.4
% Reptile			15.8			1.5

insects while on the INEL Site 0.7 and 0.2% were insects in 1975 and 1976, respectively. Since only prey remains from the nest were examined (no castings were collected), the actual mammal and insect components would be expected to be higher as both are more likely to be eaten entirely and immediately. The small number of prey remains collected undoubtedly presents a somewhat biased indication of the food habits of American Kestrels on the INEL Site.

Long-eared Owl Nesting Biology

Phenology.—Long-eared Owls were found on the Big Lost River throughout the year; but, most migrated and during the winter the number of owls was greatly reduced. Wilson (1938) found Long-eared Owls in Ann Arbor, Michigan, to be migratory while Armstrong (1958) reports that in southern Michigan, breeding areas were adjacent to winter roosts.

Using an incubation period of 21 days (Bent 1938) and a nestling period of 21.4 ± 2.9 days (determined in this study in 1976), egg-laying would have taken place from 22 through 25 May in 1975 and from the second week in April to the fourth week in May in 1976.

In 1976 the mean date of egg hatching for 11 Long-eared Owl nests was 25 May and of fledging, 14 July. There was some overlap from one nest to another as the egg-laying dates for various nests spanned up to 41 days. Hence, some Long-eared Owls were laying eggs while other pairs were fledging young.

The egg-laying dates in both years are comparable to those reported by Armstrong (1958). Reynolds (1970) found 1 nest in Oregon which contained eggs in April and Bent (1938) reports that, of 79 records in California and southern Canada, all contained eggs from 1 March to 5 June which would include the dates on the INEL Site. The egg hatching and branching dates in 1976 are also similar to those reported elsewhere (Bent 1938, Armstrong 1958, Reynolds 1970).

The young on our study area remained in the nest 21 days in 1976. Armstrong (1958) reports that at 25 or 26 days, young are sufficiently feathered to leave the nest. Since Long-eared Owls branch long before they are able to fly (Whitman 1924), investigators may mistakenly assume the early disappearance of young to be a result of juvenile mortality.

Productivity.—In 1975 we found only 3 active Long-eared Owl nests on the study area (0.1 Long-eared Owl nests/km of river); in 1976 we found 16 nests (0.6 Long-eared Owl nests/km of river). Long-eared Owls laid a mean of 3.0 ± 1.0 and 5.3 ± 0.7 eggs in 1975 and 1976, respectively, and from these 2.3 ± 0.6 and 4.2 ± 1.9 young hatched. In 1976, 5 eggs hatched in 60% of the nests and 4 or 5 young fledged in 68.8% of these nests.

Reports in the literature on the productivity of Long-eared Owls are limited. The mean clutch size on the INEL Site in 1976 is comparable to that reported by Armstrong (1958) who found an average of 4.9 ± 1.3

eggs (N = 11) per nest. Murray (1976) reported that clutch size of 18 Long-eared Owl nests in the same latitude as southeastern Idaho (40–44°N) was 4.37 eggs/clutch, which is lower than the mean clutch-size found on the INEL Site. Bent (1938) reported that clutch-size of Long-eared Owls ranged from 3 to 8 eggs and Armstrong (1958) reported a nest with 7 eggs; but, the largest clutch on our study area consisted of 6 eggs (6 nests contained 6 eggs each). Two nests failed while adults were incubating; both may have been abandoned because TC disturbed the owls during nesting. One nest was abandoned in early May but by mid-June another nest, hitherto undiscovered, was found approximately 100 m away. The nest contained recently hatched young and may have been a renesting attempt by the original pair. Bent (1938) reported a nest in which 2 broods were raised in the same year and suggested that both broods were produced by the same pair of birds.

In 1975 3 nests on the Big Lost River produced young but 1 nest was destroyed by a predator after 2 young had hatched. The 2 other nests were not found until the young had branched. These family groups consisted of at least 5 young; thus Long-eared Owls fledged an average of 1.7 ± 1.5 young/nest in 1975.

The fledging success $\frac{(\bar{x}\text{ number to fledge})}{\bar{x}\text{ number eggs}}$ on the INEL Site in 1976 was 77%. Craighead and Craighead (1956) found a success of 93% for 13 young in Moose, Wyoming and further report an average of 4.3 young produced per adult pair. Stophlet (1959) reported an average of 2.7 ± 1.5 young were found in 6 nests or in family groups around nests; but, no clutch-size data were recorded. On the INEL Site 4.1 ± 1.8 young fledged per nest in 1976.

Nest sites.—There were 18 nests attended by adult Long-eared Owls in 1976; 1 was abandoned before laying and 2 others failed during incubation. Seventeen of the nests were in old Black-billed Magpie nests. One nest was on a Black-billed Magpie nest, the top of which was indented and some fine bark was lining the recess. This was the only nest in which any modification was apparent. Bent (1938) reported that Long-eared Owls occupy old Black-billed Magpie nests.

We found 88 old Black-billed Magpie nests on the study area which appeared to be suitable for Long-eared Owl nestings, and 20% of these were used by the owls in 1976. Since Black-billed Magpies nest later than Long-eared Owls on the INEL Site, they do not seem to be competitors for nest-sites. The average height of the Black-billed Magpie nests used by Long-eared Owls was 2.2 ± 1.0 m. When incubation began a significant percent (88) of the nests had all or a portion of the canopy intact (Clopper and Pearson chart, .95 confidence belt for proportion; Dixon and Massey 1957).

Food habits.—No prey remains were recovered from Long-eared Owl nests in 1975. In 1976, a total of 97 prey remains were found at the nest sites of Long-eared Owls, 61 of which were from castings (Table 3). The danger of biasing data on food habits by counting castings that are partially composed of prey items already recorded was minimized by visiting the nest at 3 day intervals. Thus, the prey which were eaten over that period were represented in the castings as well as the few prey items which were in the nest the day of the visit.

The majority of the prey of Long-eared Owls on the INEL Site was small mammals (97.2%) which are active at night (Burt and Grossenheider 1952). *Microtus* spp. were found to be the most important prey of Long-eared Owls by Scott (1948), Armstrong (1958) and Getz (1961); but, on the INEL Site northern pocket gophers (*Thomomys talpoides*) composed the highest biomass of any prey item and accounted for 42.8% of the diet of this owl. The literature review by Marti (1976) documents northern pocket gophers as only 0.7% of the total biomass of the prey of Long-eared Owls in North America.

Ord's kangaroo rats (*Dipodomys ordii*) composed 16.5% of the diet of Long-eared Owls (or 10% frequency of occurrence) on the INEL Site which is in contrast to the 32.6% frequency of occurrence reported by Sonnenberg and Powers (1976), in southwestern Idaho. Few birds or insects were found as prey of the Long-eared Owl.

All remains of montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*), and most northern pocket gophers were found in castings but not as prey items in the nest. Since most nests were visited during the morning, these prey may have already been consumed while Ord's kangaroo rats and deer mice (*Peromyscus maniculatus*) had not, perhaps because they were captured in the early morning. This suggests that if quantitative data on food habits of nocturnal raptors is desired, the investigator should visit the nest at night.

Since Long-eared Owls are adapted to hunt in open areas (Getz 1961, Marti 1976), the Big Lost River with its abundance of nest-sites is an ideal nesting area. Why then were there fewer active nests found in 1975 on the INEL Site? The influence of the cooler, wetter weather in 1975 or a decrease in available prey may have been responsible. Hagen (1965) reports that in Norway, Long-eared Owl populations and productivity are linked to micro-rodent cycles. However, Marti (1974) reports that local populations of Long-eared Owls fluctuate; they are in an area 1 year but gone the next. Thus, the apparent increase in the nesting population on the

TABLE 3

PREY REMAINS FOUND IN 13 LONG-EARED OWL NESTS ON THE INEL SITE IN 1976, COMPILED FROM PREY AND CASTINGS FOUND AT THE NEST

	N	Biomass (g)	% Biomass
Ord's kangaroo rat (*Dipodomys ordii*)	10 (3)[1]	555.0	16.5
Deer mouse (*Peromyscus maniculatus*)	29 (9)	493.0	14.6
Montane vole (*Microtus montanus*)	14 (14)	483.0	14.3
Great Basin pocket mouse (*Perognathus parvus*)	19 (19)	285.0	8.5
Northern pocket gopher (*Thomomys talpoides*)	19 (14)	1444.0	42.8
Shrew (*Sorex* sp.)	1 (1)	18.0	0.5
Unidentified birds	4 (0)	96.0	2.8
Insect	1 (1)	0.6	< 0.1
Total	97 (61)	3374.6	100.0

[1] Parenthetical numbers represent remains found in castings.

INEL Site may be accredited to a vacillating local population of Long-eared Owls.

SUMMARY

The nesting biology of the American Kestrel and the Long-eared Owl was studied during 1975 and 1976 along the Big Lost River on the INEL Site in southeastern Idaho. In 1975 the mean clutch-size of American Kestrels was 4.5 eggs/clutch ($N = 13$) and in 1976 it was 4.7 eggs/clutch ($N = 23$). Long-eared Owls laid a mean of 3.0 eggs/nest ($N = 3$) in 1975 and 5.3 eggs/nest ($N = 15$) in 1976. The productivity of American Kestrels was 3.7 young/nest in 1975 and 4.0 young/nest in 1976. The productivity of Long-eared Owls was 1.7 young/nest in 1975 and 4.1 young/nest in 1976.

Avian prey composed the majority of the diet by biomass of American Kestrels in 1975 and 1976. Changes in the percent mammalian and reptilian prey occurred during these years. Mammalian prey made up 97.2% of the total diet by biomass of Long-eared Owls in 1976. Northern pocket gophers composed the highest percent in biomass.

There was an increase in American Kestrel nests found on the INEL Site from 1975 to 1976 and an increase in Long-eared Owl nests in the same year. The reasons for the increase of both species may be the same—adverse weather conditions in 1975 and/or

an increase in available prey. Other reasons may also have been responsible. There were more American Kestrel nest-sites in 1976 than in 1975 since the number of nesting boxes erected on the Big Lost River was increased and local Long-eared Owl populations have been known to fluctuate.

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ORGANOCHLORINE POLLUTANTS AND POPULATION STATUS OF LEAST TERNS IN SOUTH CAROLINA

Lawrence J. Blus and Richard M. Prouty

Most populations of Least Terns (*Sterna albifrons*) in the United States are reportedly declining or experiencing poor reproductive success (Fisk 1975, Massey 1974). The California race (*S. a. browni*) is classified as "endangered" by the U.S. Fish and Wildlife Service (Wilbur 1974) and the eastern race (*S. a. antillarum*) is classified as "threatened" by the State of Florida. Interior Least Tern (*S. a. athalassos*) populations are apparently experiencing much the same problems as those of the other races (R. Downing, pers. comm.). Little Tern (*S. a. albifrons*) populations in Great Britain and Ireland have steadily decreased since the early 1930's (Norman and Saunders 1969).

Sprunt and Chamberlain (1949), in the last evaluation of the Least Tern in South Carolina described its population status as "completely satisfactory." Recent concern about the future of the Least Tern and the need for updating its status in South Carolina prompted us to study its population status and reproductive success in that state, particularly in relation to organochlorine pollutants.

METHODS

We studied Least Tern colonies on the Cape Romain National Wildlife Refuge (CRNWR) and surrounding areas in South Carolina from 1971 through 1975. Each year, we were in the field from April to August. Because most of our effort was directed toward studying Brown Pelicans (*Pelecanus occidentalis*) and other estuarine birds, we spent only a limited amount of time surveying for new Least Tern colonies and studying those that were located. But when a colony was located, we attempted to count all nests with eggs or young; empty nest scrapes were sometimes also counted. We visited several colonies only once a season, and we rarely visited a colony more often than once a week. Because of our infrequent visits and the difficulty in locating the young, we were only able to roughly estimate reproductive success (fledglings per nest) as follows: good $= \geqslant 1$, fair $= 0.50$–0.99, poor $= < 0.50$, and failed $= 0.00$.

Eggs were collected from 4 colonies in 1972–1975. We took 1 egg from 38 nests selected for sampling and collected 6 eggs that were washed out of nests by tidewaters. We collected eggs in all sections of each sampled colony in order to obtain a representative sample. We weighed and measured the eggs soon after collection. The contents of the eggs were placed in glass bottles that were previously rinsed with a dilute nitric acid solution, deionized water, hexane, and acetone; aluminum foil-lined caps were attached; and then the samples were frozen. The shells were thoroughly washed with tap water and allowed to dry at room temperature. Shell thickness (shell and shell membranes) was measured at 3 sites on the waist of each egg with a micrometer graduated to 0.01 mm. The mean of the 3 measurements was used to represent the thickness of the shell.

Contents of eggs were analyzed for organochlorine residues by electron capture gas chromatography. A 4% SE-30/6% QF-1 column was used for the 1972 samples and a 1.5% OV-17/1.95% QF-1 column was used for the 1974 and 1975 samples (Cromartie et al. 1975). The level of sensitivity was 0.50 μg/g for PCB's and 0.10 μg/g for other organochlorines.

RESULTS

Surveys of nesting colonies and reproductive success.—We found Least Tern nesting colonies in 6 different sites on the CRNWR (3 on Cape Island, 2 on Raccoon Key, and 1 on Anderson Creek Shellbank), and on 4 nearby islands on the Atlantic Coast (Table 1). Fisk (1975) reported Least Terns nesting several miles inland from Charleston, South Carolina in 1974. They reportedly nested on black polyethylene plastic at an agricultural research station. In 1976 and 1977, Least Terns established 3 colonies on flat-roofed buildings in Charleston (E. J. Fisk, pers. comm.). All other known colonies of Least Terns in South Carolina are on coastal islands; adults are rarely seen inland (Sprunt and Chamberlain 1949).

Least Terns are colonial nesters that select barren sand or shell beaches for nesting. The terns scrape out a cavity in the bare sand or arrange a pile of small shells where they lay their eggs. Marples and Marples (1934) indicated that Little Terns characteristically excavate more scrapes than required for nesting. On 18 June 1975, we found 555 fresh scrapes and 71 nests with eggs on the southwest point of Cape Island; 220 active nests were eventually found in this colony. On the same date, 379 fresh scrapes and 25 nests with eggs were noted in the colony on Cape Island Point; 26 active nests were eventually found. Similar ratios of scrapes to active nests were also found in the other colonies.

Seven of the 10 nesting areas of Least Terns located in South Carolina were near—but did not overlap—those of the Black Skimmer (*Rynchops nigra*) and Gull-billed Tern (*Gelochelidon nilotica*). The minimum distance between Least Tern nests and nests of their larger associates was about 15 m. The Least Tern nested near the Wilson's Plover (*Charadrius wilsonia*) in 3 colonies, although we only found about 8 plover nests. In North Carolina, nesting areas of Least Terns also did not overlap those of other colonial nesting species (Soots and Parnell 1975).

The color of the small eggs and young of the Least Tern is such an effective camouflage that it is difficult to locate them against the background of sand and shells. Censusing is difficult because the terns tend to nest in loose aggregations where their nests may be 3 to 4 m apart, the colony may be divided into several discontinuous subcolonies, and because the precocial young usually leave the colony when only a few days old. The most effective method of finding nesting colonies is to check for adult activity on likely looking beaches, shell banks, or dredge islands.

Migrating Least Terns arrive in South Carolina as early as 15 March (Sprunt and Chamberlain 1949); they apparently initiate reproductive behavior sometime in April. We found empty scrapes as early as 3 May in an area that later contained active nests. Eggs were found as early as 17 May and young as early as 6 June. We found eggs as late as 24 July.

The number of eggs in 396 clutches ranged from 1 to 3 ($\bar{x} = 1.73$). These clutches were in colonies that were censused several times before hatching. Of the 396 clutches, 116 (29.3%) contained 1 egg, 272 (68.7%) contained 2 eggs; and 8 (2.0%) contained 3 eggs. The peak of hatching was between 21 June and 8 July in the colony on Cape Island Point in 1971, and between 10 and 24 July in 2 colonies, Cape Island Point and Cape Island (southwest point), in 1975. The nesting season of the Least Tern is relatively short and although this species may renest when their eggs are lost (Schönert 1961), they do not extend their nesting season into August and September in South Carolina as the Gull-billed Tern and Black Skimmer sometimes do after repeated nesting failures.

We estimated good reproductive success in 1 colony, fair success in another colony, and we classified reproductive success in the remaining colonies as poor, unknown, or failed (Table 1). Even in the 2 colonies where reproductive success was estimated as good or fair, we observed no young in the colony after the peak of hatch. For example, 102 nests were counted on 21 June and 112 young (28 out of nests) were observed on Cape Island Point in 1971; we estimated the colony contained 150 nests. On our next visit on 8 July and subsequent visits, no active nests or young were observed. Also, 220 nests were counted on 2 July on the southwest point of Cape Island: 137 nests and 44 young (28 out of nests) were observed on 10 July. On the next visit on 24 July and subsequent visits, no active nests or young were observed. The colony on the southwest point of Cape Island in 1975 contained the largest number of active nests (220) of any colony that we censused.

Least Tern nests are susceptible to flooding, predation, and disturbance. We observed tidal flooding of nests in 4 colonies, and suspected that at least some of the nests in other colonies were also susceptible to flooding. In the second week of June 1975, all nests in 2 colonies on Cape Island were destroyed by tidal flooding. Of the 61 active nests present on Cape Island Point on 28 May, only 9 abandoned eggs (2 depredated) remained on 12 June. By 18 June, many of the Least Terns had renested; we found 71

TABLE 1

CENSUSES OF LEAST TERN COLONIES, CAPE ROMAIN NATIONAL WILDLIFE REFUGE AND SURROUNDING AREAS

Colony	Year	Number of active nests[1]	Estimated reproductive success[2]
Cape Island Point	1971	102+	Good
	1972	Apparently inactive	—
	1973	2+	Poor
	1974	99	Poor
	1975	26	Poor
Cape Island (southwest point)	1971	Not censused	—
	1972–73	Apparently inactive	—
	1974	69	Unknown
	1975	220	Fair
Cape Island (south end)	1972	Terns nesting–not censused	—
		Inactive other years	—
Raccoon Key (north end)	1971	Not censused	—
	1972	32	Failed
	1973	19	Poor
	1974	1+	Poor
	1975	Apparently inactive	—
Raccoon Key (south end)	1972	1+	Unknown
		Inactive other years	
Anderson Creek Shellbank	1971	Not censused	—
	1972	11	Poor
	1973	2	Unknown
	1974	Not censused	—
	1975	Inactive	—
Capers Island (Charleston County)	1974	3+	Unknown
		Not censused other years	—
Sullivans Island	1971–73	Not censused	—
	1974	13	Poor
	1975	Nests not censused; 10 fledglings on beach on 18 July (see text)	—
Bird Key (Stono River)	1971–72	Not censused	—
	1973	66+	Unknown
	1974	3+	Poor
	1975	8	Poor
Deveaux Bank	1971–74	Apparently inactive	—
	1975	1+	Failed

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[1] Maximum number of nests counted during one day; a "+" indicates that the census was incomplete.

[2] See text for explanation.

active nests on the southwest point and 9 active nests on Cape Island Point. A number of terns losing nests on Cape Island Point apparently moved to the southwest point to renest. By 10 July, some nests on the southwest point were flooded and 8 abandoned eggs were located; although the flooding was relatively minor and a number of active nests and recently hatched young were present.

We noticed some evidence of predation of Least Tern eggs and young, but we found no sign of predation on the few dead adults located. Ghost crabs (*Ocypode quadrata*) are numerous in most Least Tern colonies and are probably important predators of eggs and young. Several young terns were observed hiding in crab burrows. Ghost crabs are suspected of taking eggs and young of birds (Beckett 1966, Sprunt 1948), and we observed a ghost crab preying on a young Gull-billed Tern. Rats (*Rattus* spp.), raccoons (*Procyon lotor*), snakes, and several birds of prey were also observed on the nesting islands and are potential predators of Least Terns.

In contrast to other colonial birds in South Carolina, Least Terns sometimes nest in areas heavily used by man. The colony on Sullivans Island was on a beach regularly used by bathers and dogs. Success in 1974 was apparently poor, but 10 fledglings were observed near the colony site on the only visit in 1975. Massey (1974) indicated that Least Terns may move some distance soon after fledging; thus, it is uncertain that the fledglings observed on Sullivans Island were actually raised there. Other sources of disturbance to nesting terns include livestock (Capers Island) and loggerhead turtles (*Caretta caretta*).

Eggshell thickness.—The mean eggshell thickness of Least Tern eggs ranged from 2 to 7% thinner than the thickness of eggs collected before 1947 (Table 2). Individual eggshell thickness ranged from 0.13 to 0.18 mm in the pre-1947 sample and from 0.13 to 0.17 mm in the sample collected in the 1970's. Although multiple range tests (Duncan 1955, Kramer 1956) indicated a significant difference ($P < 0.05$) between the pre-1947 mean and the 1974 mean, further statistical testing revealed that the sample size was insufficient to detect a change of 10% when probability = 0.05, power = 0.8, and the coefficient of variation = 7.9% (Sokal and Rohlf 1969:247, Klaas et al. 1974). We observed no extremely thin-shelled, cracked, or crushed eggs.

Organochlorine residues.—Residues of DDE and PCB's were found in each of the 44 eggs analyzed (Table 3). Low levels of mirex, dieldrin, *trans*-nonachlor, and toxaphene were found in a few eggs. Residues analyzed for, but not detected, included hexachlorobenzene, *cis*-nonachlor, *cis*-chlordane, oxychlordane, heptachlor epoxide, and endrin.

Residues of DDE declined each year of the study so that residues in 1975

TABLE 2

EGGSHELL THICKNESS OF LEAST TERN EGGS

Eggshell thickness (mm)			
Pre-1947	1972	1974	1975
0.152±[1]	0.145±	0.142±	0.149±
0.002	0.005	0.002	0.004
(61) A	(11) A	(20) A	(15) A

[1] Mean ± standard error, sample size in parentheses. When means share a common letter, this indicates that those means are not significantly different ($P > 0.05$) from one another as calculated by multiple range tests (Duncan 1955, Kramer 1956) or the multiple range tests indicated significant differences but other tests (Sokal and Rohlf 1969; Klaas et al. 1974) revealed the sample size was too small (see text).

were nearly 50% lower than in 1972. Although multiple range tests (Duncan 1955, Kramer 1956) indicated a significant difference ($P < 0.05$) between means for DDE in each of the 3 years (Table 3), further statistical testing revealed that, except for the comparison of the 1972 and 1975 means, the sample size was insufficient to detect the observed percentage change in means when probability = 0.05, power = 0.8, and the coefficient of variation = 37% (Sokal and Rohlf 1969:247). Significant differences ($P < 0.05$) were found between mean PCB residues in each of the 3 years,

TABLE 3

RESIDUES OF ORGANOCHLORINE POLLUTANTS IN LEAST TERN EGGS

		µg/g (fresh wet weight)[1]	
Year	Sample size	DDE	PCB's
1972	9	0.63[2] A[3]	0.40 A
		0.48–0.80	0.18–0.65
		0.39–1.06	0.25–1.10
1974	20	0.48 AB	1.08 B
		0.39–0.57	0.95–1.22
		0.19–1.22	0.67–1.90
1975	15	0.33 B	0.62 C
		0.27–0.39	0.51–0.75
		0.22–0.53	0.25–1.03

[1] Other organochlorine residues detected included mirex (0.12 µg/g in 1 egg), *trans*-nonachlor (0.10 µg/g in 1 egg), dieldrin (0.10 µg/g in 1 egg), and toxaphene (0.10 µg/g in 1 egg and 0.40 µg/g in another).

[2] Geometric mean (first line), 95% confidence limits (second line), and range (third line).

[3] See Table 2 and text for explanation of letters.

and the sample size was sufficient to detect the observed percentage change in means when probability = 0.05, power = 0.8, and coefficient of variation = 39%. In contrast to the steady decline in DDE residues, PCB residues increased from 1972 to 1974 then declined in 1975 (Table 3).

DISCUSSION

We found no evidence of a decline in South Carolina Least Tern populations since the 1940's. Sprunt and Chamberlain (1949) indicated the Least Tern had recovered from exploitation by 1927; they estimated 600 breeding pairs occurred within 80 km of Charleston. We were among cooperators surveying nesting colonies of Least Terns along the entire South Carolina coast; these surveys recorded 691 breeding pairs in 1974 and 628 pairs in 1975 (Fisk 1975, E. J. Fisk, pers. comm.). The population figures before the 1970's were based mainly on estimates, and covered only a portion of the coastline. Apparently, the South Carolina population was never very large. Least Terns in South Carolina are probably not producing sufficient young to maintain a stable population, but our data are severely limited and intensive research on reproductive success and age specific mortality rates are required to determine population status. Because of the logistical problems of studying Least Terns, there is little quantitative information on reproductive success of these birds. A colony of Least Terns near Gulfport, Mississippi, apparently experienced an excellent rate of reproductive success in 1976; over 400 young and nearly 200 nests with eggs were observed in late June (Jackson 1976).

Declines of Least Tern populations have been documented in other states. A single island in Georgia contained an estimated 2500 breeding pairs in 1925 (Tomkins 1959); 2 nests were located in the entire state in 1974 (Fisk 1975). An estimated 25,000 terns occupied the North Carolina coast in 1939 (Pearson et al. 1942). The estimate by Pearson et al. seems much too high since they found only 830 nests. Downing (1973) estimated 1138 pairs of Least Terns in North Carolina in 1973 whereas Fisk (1975) estimated 463 pairs in 1974. The North Carolina population has probably declined over the last 40 years due to loss of several nesting colonies, but the decline has probably been far less drastic than commonly believed (Nisbet 1973). The decline of the Georgia population was probably caused by man-made alterations in nesting grounds that permitted invasion of raccoons and other predators (Tomkins 1959). Human interference has also played a major role in the decline of Least Tern populations in California (Massey 1974, Wilbur 1974), Massachusetts and other localities on the Atlantic Coast (Nisbet 1973), and in Great Britain and Ireland (Norman and Saunders 1969).

Residues of organochlorine pollutants found in eggs of Least Terns from South Carolina are low and pose no identifiable threat to the birds. Massey (1971) found DDE in abandoned eggs of Least Terns collected in Orange County, California, in 1970. She reported residues of DDE ranging from 42 to 271 μg/g on an apparent lipid basis which we converted to 6 to 41 μg/g on a wet weight basis. Although Massey (1971) made no attempt to interpret relevance of these residues, they probably posed a threat to the Least Terns in Orange County as residues of that magnitude induced adverse effects on reproductive success of Common Terns (*Sterna hirundo*) in Canada (Fox 1976). Least Tern eggs collected in Texas in 1970 contained an average of 6.9 μg/g of DDT and metabolites and 2.6 μg/g of PCB's on a wet weight basis (King et al. 1978).

The declining trend in DDE residues and erratic trend for PCB residues in eggs of Least Terns from 1972 through 1975 were similar to trends of these pollutants in Brown Pelican eggs collected in South Carolina during the same period (Blus et al. 1977, Blus et al. unpublished data). Least Tern eggs contained lower residues than those of the Brown Pelican and other estuarine birds in South Carolina (Blus et al. unpublished data).

We are guardedly optimistic about the future of Least Terns in South Carolina. The colonies on Cape Island, Raccoon Key, and Anderson Creek Shellbank are protected by the CRNWR. Capers Island is now managed by the South Carolina Conservation Department; Deveaux Bank is managed by the National Audubon Society and has been designated the Alexander Sprunt, Jr. Sanctuary. Bird Key (Stono River) is owned by the state but is not managed by the Conservation Department. The future of the colonies on Kiawah Island, Hilton Head Island (not covered in this report), and Sullivans Island is tenuous because of extensive human disturbance. A good set of management measures outlined by Buckley and Buckley (1976) should be followed to ensure protection of Least Terns nesting on developed beaches. Several of the colonies have been posted, but for best results, close surveillance must accompany the posting. The recent roof nesting adaptation of the Least Tern seems a favorable one as the birds are free from most predators and human disturbance; however, flooding is a problem. Management possibilities for roof nesters include nesting containers (several inches high) containing sand or shells and simple structures that could provide cover for the young.

SUMMARY

Least Tern nesting colonies on the Cape Romain National Wildlife Refuge and surrounding areas in South Carolina were studied from 1971 through 1975. We located 10 colonies

including 6 on the Refuge and 4 on nearby coastal islands. The number of nests in each colony ranged from several up to 220.

Least Terns began reproductive activity in April, and the egg-laying period ranged from May to July. The earliest hatching record was 6 June. Reproductive success in most colonies seemed poor. Tidal flooding of eggs, predation of eggs and young, and disturbance by domestic animals and man were responsible for most failures.

Residues of DDE, PCB's, and other organochlorine pollutants in the eggs were low and posed no identifiable threat to the Least Terns. DDE residues in eggs declined from 0.63 μg/g in 1972 to 0.33 μg/g in 1975. In contrast, PCB residue trends were erratic; mean residue values were 0.40 μg/g in 1972, 1.08 μg/g in 1974, and 0.62 μg/g in 1975.

Eggshell thickness means for 1972, 1974, and 1975 were 2 to 7% lower than the pre-1947 mean; but the differences between means were not statistically significant.

There is no evidence of a decline in Least Tern populations in South Carolina over the past 30 years such as observed in many other parts of the range of the species. A number of the current nesting islands seem secure from adverse environmental perturbations, although several colonies are on islands that are in danger of extensive development.

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RADIONUCLIDE CONCENTRATIONS IN NESTLING RAPTORS NEAR NUCLEAR FACILITIES

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The presence of some pollutants in raptors and the importance of raptors as indicators of environmental contaminants have been documented (Olendorff 1973). Literature on radionuclide concentrations in birds near nuclear facilities deals mainly with passerine species (Willard 1960) or waterfowl (Brisbin et al. 1974). The only available literature on raptors concerns radioiodine in thyroids (Hanson and Kornberg 1956). We conducted a study to determine the level of contamination by gamma-emitting radionuclides in nestling raptors near 2 nuclear facilities at the Idaho National Engineering Laboratory Site.

MATERIALS AND METHODS

The study was conducted from May through July 1976 on the Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho. Big sagebrush (*Artemisia tridentata*) and grass (*Agropyron dasystachyum* and *Stipa comata*) are the predominant vegetation types on the study area.

Raptors were studied near 2 nuclear facilities, the Test Reactor Area (TRA) and the Idaho Chemical Processing Plant (ICPP). TRA is an advanced nuclear materials testing complex. Radioactive liquid waste from the TRA facilities is placed in two 1.5 ha leaching ponds. Approximately 46,400 curies (Ci) of beta-gamma activity were introduced into the ponds from 1952 to 1976. During the study period, 532 Ci of liquid beta-gamma radioactive waste were released from TRA facilities; 11% of this consisted of nuclides with half-lives greater than 1 year. In addition, a smaller sanitary waste disposal pond is located near TRA.

The ICPP recovers uranium from spent nuclear fuels and processes the resultant liquid waste into noncorrosive solid form. During operations, the ICPP releases radionuclides into the atmosphere, and in 1976, 0.04 Ci of particulate airborne waste containing 0.02 Ci of cesium-137 were released. During 1976, average atmospheric radioactivity at the INEL Site boundaries was not statistically different from concentrations in control or background areas (U.S. Energy Research and Development Administration 1977). However, the soil in the vicinity of the ICPP contains above background levels of radioactivity (Bowman et al. 1976).

The Big Lost River flows intermittently across the INEL Site for approximately 50 km; cottonwood trees (*Populus deltoides*) which grow on its banks provide nesting sites for American Kestrels (*Falco sparverius*) and Long-eared Owls (*Asio otus*), the most numerous nesting raptors along the river. We searched the area along the Big Lost River for nesting raptors and all American Kestrel and Long-eared Owl nests located within 1.5 km of ICPP or TRA were studied. Seven other nests downstream and 4 nests upstream of the facilities and a Marsh Hawk (*Circus cyaneus*) nest near the sanitary waste disposal pond near TRA were also studied. In addition to natural nest cavities, sampling locations were created by placing 5 American Kestrel nesting boxes (Hamerstrom et al. 1973) near the facilities. Seventeen raptor nests were studied and 2 young from each nest were temporarily removed for analysis. The American Kestrels were analyzed when they were 20 days old and the Long-eared Owls when they were 15 days old. The Marsh Hawks were analyzed twice, at 11 and 21 days of age.

Each young was placed in a ventilated 1800 ml plastic container with absorbant material and analyzed for gamma-emitting radionuclides on a 65 cm^3 germanium-lithium crystal (within a shielded chamber) connected to a multichannel analyzer. Raptors were gamma counted for 30 min and then returned to their nests. Although they were away from the nest a total of 2 h, the process appeared to cause no harm to any of the young birds.

Food habits were determined by visiting each nest site every 3 days and identifying material in castings and prey remains found at the nest. Rodents were snap-trapped at the TRA ponds and were analyzed for radionuclide content by whole-body gamma scans.

Internal doses to raptors were calculated (Martin 1976) assuming the internal radionuclides were in equilibrium with the body and uniformly distributed throughout the body.

RESULTS

Whole-body gamma scans of young raptors (Table 1) indicated that birds from nests near TRA and ICPP had higher concentrations and a larger variety of gamma-emitting radionuclides than those from other locations. Cesium-137 occurred in all birds in which radionuclides were detected and had the highest concentration of any radionuclides. It was the only radionuclide detected in birds near ICPP. Birds analyzed from nests near TRA contained up to 9 radionuclides (selenium-75, cesium-137 and -134, niobium-95, iodine-131, cobalt-60, zinc-65, barium-140 and lanthanum-140). The highest total activities were found in the Marsh Hawk and American Kestrel nestlings at TRA; 87 and 44 picocuries (pCi) per gram, respectively ($pCi = 3.7 \times 10^{-2}$ disintegrations/sec). Only young from nests near facilities had detectable amounts of radionuclides. The young Marsh Hawks were analyzed twice over a 10-day period, during which both radionuclide concentration and the number of nuclides in the nestlings increased.

Prey remains and feces from 2 American Kestrel nests were gamma scanned after the young had fledged. Seventeen radionuclides were detected. The radionuclides common to both the young from these nests and in the fecal and prey remains were of the same order of magnitude. Most of the radionuclides detected in the prey remains and feces as well as in the young raptors from the TRA area were also present in rodents (deer mouse [*Peromyscus maniculatus*]; least chipmunk [*Eutamias minimus*]; Ord's kangaroo rat [*Dipodomys ordii*]) captured near the TRA radioactive leaching ponds. These animals were all represented in the prey remains and castings of the American Kestrel: 2.7% were deer mice, 17.8% were chipmunks, and 1.4% were kangaroo rats. The mean concentration of radionuclides in

TABLE 1

RADIONUCLIDE CONCENTRATIONS IN AMERICAN KESTRELS, LONG-EARED OWLS, AND MARSH HAWKS IN RELATION TO DISTANCES FROM NUCLEAR FACILITIES ON THE INEL SITE*

Species	Distance km	(Facility)	Number of radionuclides detected	Activity (pCi/g) Bird 1	Activity (pCi/g) Bird 2
Marsh Hawk (1st count)	0.1	(TRA)	9	1.3	1.5
Marsh Hawk (2nd count)	0.1	(TRA)	9	35.0	87.0
American Kestrel	0.1	(TRA)	8	44.0	11.0
American Kestrel	0.2	(TRA)	3	1.3	3.3
American Kestrel	1.0	(ICPP)	1[a]	0.8	0.3
American Kestrel	1.0	(ICPP)	1	0.4	0.6
Long-eared Owl	1.4	(ICPP)	1	0.0[b]	0.0
Long-eared Owl	1.6	(ICPP)	1	ND[c]	0.4
Long-eared Owl	2.0	(ICPP)	0	ND	ND
Long-eared Owl	2.6	(ICPP)	1	0.3	0.2
Long-eared Owl	3.5	(ICPP)	1	ND	0.3

* No nuclides were detected in 2 young from each of 5 Long-eared Owl nests located from 4.2 to 12.5 km from ICPP or in 2 young from each of 2 American Kestrel nests located 6.6 and 11.2 km, respectively, from ICPP.

[a] Those with 1 detected radionuclide contained only Cs-137.

[b] Nuclide detected, but value not determined.

[c] ND = No nuclides detected.

rodents was approximately 4 to 290 times greater than in the raptors at TRA (deer mice, 381 pCi/g; least chipmunks, 68 pCi/g; Ord's kangaroo rats, 4 pCi/g).

Based on the radionuclide concentrations at the time of analyses, doses to raptors from internal gamma-emitting radionuclides ranged from 0 to 0.1 mrem/day (mrem is a unit of absorbed dose equivalent).

DISCUSSION

Young birds from 1 Marsh Hawk and 2 American Kestrel nests nearest TRA contained the highest radionuclide concentrations (Table 1). However, the concentrations encountered in the raptors were lower than those found in potential prey items collected near the TRA ponds. Since the contamination at the TRA ponds is primarily contained within a 2.6 ha area of the pond complex, other prey within the home range of the raptors in the TRA vicinity contained only cesium-137 at background concentrations of 0.3 pCi/g. Therefore the raptors likely fed on prey both from the TRA pond area and from noncontaminated areas.

The increase in body burdens of young Marsh Hawks over a 10-day period suggests that they fed on radioactively contaminated prey or consumed a more contaminated prey item prior to the later gamma counting. Since the nuclides that were detected in these nestlings were found in the TRA pond prey species and the young birds were confined to the nest, we presumed the raptors were being contaminated through their food. However, we could not conclude that the nestlings were fed prey items exclusively from the contaminated area.

All remaining young which had detectable radionuclides contained only Cs-137 with a minimum detection limit of 0.02 pCi/g ($P = 0.05$). The average Cs-137 concentrations in nestling raptors was 1.8 pCi/g. Average Cs-137 concentrations in passerine birds from the Oak Ridge National Laboratory White Oak Lake Bed in Tennessee were 12 to 1550 times higher than in the birds in this study (Willard 1960). Coots (*Fulica americana*) from a cooling reservoir at the Savannah River Plant in South Carolina had Cs-137 concentrations 2 to 4 times higher than nestling raptors studied at the INEL (Brisbin et al. 1974).

Some Cs-137 may be expected in all nestlings since it is an ubiquitous component of world-wide fallout. Young raptors containing detectable amounts of Cs-137 were from nests located adjacent to or within 3.5 km northeast of ICPP. Birds from the nests farther northeast or southwest of ICPP did not contain detectable concentrations of radionuclides (Table 1). The predominant winds on the INEL Site are from the southwest. Since ICPP releases Cs-137 into the atmosphere, and the soils near ICPP have detectable concentrations of Cs-137, we concluded that the Cs-137 body burdens in nestling raptors northeast of the facility have resulted from effluents at ICPP. Previous studies on pronghorns (*Antilocapra americana*) (Markham et al. 1976) and Mourning Doves (*Zenaida macroura*) (Markham 1976) have shown that elevated Cs-137 muscle concentrations in these species near ICPP were due to ICPP atmospheric releases.

The maximum dose received by raptors from internal radionuclides was 0.10 mrem/day which is less than ¼ of the natural background radiation for this area (0.45 mrem/day, U.S. ERDA 1977). Due to the small dose from internal radionuclides and the short time young raptors are exposed to them, no injurious radiation effects would be expected.

A high uncertainty (± 25%) was associated with our gamma counting method. This uncertainty resulted because our instruments were not calibrated for such irregularly shaped specimens and because the distribution of the radionuclides in the bodies of the raptors was unknown. However, the data are available for indicating which radionuclides are present and the relative magnitude of the concentrations.

SUMMARY

Young raptors from nests near a nuclear reactor facility and a nuclear fuel reprocessing plant in Idaho were studied to determine the concentrations of gamma-emitting radionuclides in them. Young from nests close to the Test Reactor Area (TRA) showed the highest concentrations and largest variety of radionuclides of any birds studied. Since the same radionuclides were present in potential prey items collected near the radioactive leaching ponds and in samples of fecal material and prey remains from the nests, we concluded that the radionuclides originated at the radioactive leaching pond near TRA and were passed to the raptors through their prey. However, the concentration of radionuclides in raptors was much lower than in prey items from the TRA pond. Our data indicated that although radionuclides were transferred to higher trophic levels, the concentrations were diluted considerably by consumption of uncontaminated rodents. Raptors which nested immediately downwind of or near the Idaho Chemical Processing Plant (ICPP) showed detectable concentrations of Cs-137. Since the soils around ICPP were contaminated with low levels of Cs-137 and ICPP released Cs-137 to the atmosphere, the concentrations in these nestlings probably was due to atmospheric release of radioactivity from this facility. We concluded from our data that the influences of ICPP and TRA on radionuclide concentrations in nestling raptors were limited to an area within 3.5 km of the facilities.

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ACTIVITIES OF RADIO-EQUIPPED COMMON GRACKLES DURING FALL MIGRATION

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Large numbers of migrant Common Grackles (*Quiscalus quiscula*) roost each fall at Tishomingo National Wildlife Refuge, on the north end of Lake Texoma, in south-central Oklahoma (Fig. 1). There they damage windrowed peanuts left to dry in surrounding farmland (Mott et al. 1972). A radiotelemetry study was conducted in November 1971 and 1972 to obtain information on daily activities of individual Common Grackles, and thereby gain a clearer understanding of the peanut damage problem. This paper stresses the behavior of individual birds over periods of time as distinct from impressions of what general populations appear to do when merely visually observed.

STUDY AREA AND METHODS

The study area encompassed Atoka, Bryan, Johnston, and Marshall counties in Oklahoma, and Fannin and Lamar counties in Texas. Peanuts, cotton, sorghum, wheat, and oats are major crops, and pastures are scattered through this area. Hardwoods, particularly oak (*Quercus* spp.), cover stream bottoms and hilly areas.

Three blackbird roosts were present in marshes on or near the refuge. In 1971, birds used the Nida Point and Headquarters roosts (5.3 km apart), and in 1972 the Nida Point and Bee roosts (5.1 km apart, Fig. 1). The estimated roosting population of Common Grackles, Red-winged Blackbirds (*Agelaius phoeniceus*), Brown-headed Cowbirds (*Molothrus ater*), and Starlings (*Sturnus vulgaris*) varied from 15,000 to 2,300,000 birds.

Ten of the heaviest grackles were selected from birds trapped or mist-netted near their roosts. Based on plumage iridescence and size, all 10 grackles were sexed as males. Due to the color of the iris and underwing coverts, they were aged as unknowns. Each was weighed, marked with a 3.7 × 2.5 cm plastic tag attached to the U.S. Fish and Wildlife Service leg band, instrumented with a 164 MHz transmitter (Kolz and Corner 1975) attached to the middle 4 retrices, and released. Transmitters and clips weighed an average of 3.9 g, or 3.3% of an average bird's weight (119 g).

Birds were monitored from ground vehicles or a Cessna 150 airplane with portable receivers and hand-held or vehicle-mounted antennas (Bray 1974). Trackers usually sighted the flock containing a radio-equipped grackle, and sometimes the bird itself. Locations of birds were marked on topographic maps. Birds were occasionally followed throughout a day, but they were usually monitored intermittently because of equipment repair and other interferences.

The area that grackles occupied between early morning and late afternoon movements has been termed the "major diurnal activity range" (MDAR, Bray et al. 1975). The geometric center of activity was determined for each MDAR by the method of Hayne (1949). In determining the center of activity, we used only fixes that differed from the previous fix (Hayne 1949, Tester and Siniff 1965). We calculated the mean activity radius of the MDAR by the method of Dice and Clark (1953). Mean activity radii of MDARs were determined only for the days that trackers checked on instrumented birds throughout the day.

Home ranges were delineated by connecting perimeter fixes and flight routes, and this area was measured with a compensating polar planimeter. Home range in this study refers to the home range during the period of tracking.

The Nida Point roost (Fig. 1) was chosen as a reference location on the refuge from which all bird locations could be measured, since it was the area most heavily used by roosting grackles.

RESULTS AND DISCUSSION

The 10 birds were monitored for 63 bird-days (3 to 10 days per bird). On some days a bird was located only at the roost or only in the MDAR. No data pertaining to the first day and night after instrumentation of each bird are presented in this paper because birds moved shorter distances from the roost on the first day of monitoring than on subsequent days ($P < 0.01$, 2-way ANOVA with orthogonal comparisons). No bird was monitored longer than 9 days after the 1-day adjustment period. Observed movements and activities of instrumented birds did not differ from those of other grackles after the first day.

Roosts.—Seven grackles were monitored at roosts in the refuge area on 40 bird-nights. They spent 38 bird-nights in 3 marsh roosts and 2 bird-nights in wooded areas 3.5 and 6.3 km from the Nida Point roost. Three of the 7 switched marsh roosts on 10 occasions, or 2 to 4 times per bird.

The other 3 grackles migrated soon after they were instrumented, and subsequently were located on 6 bird-nights in 5 different roosts. Distances between their roosts on successive nights ranged from 9.3 to 52.8 km, and the roosts were located from 41.5 to 96.9 km from the Nida Point roost. Distance between the Nida Point roost and successive roosts did not increase each day, as one might suspect with a migrating bird. For example, 1 grackle roosted 96.9, 65.2 and 56.8 km from the Nida Point roost on successive nights.

Movements between roost and MDAR.—Instrumented grackles always left the roost with the rest of the roosting population. On 12 of 16 mornings when 2 radio-equipped birds left at different times, the first bird out had a center of activity farther from the roost than the second one. Bray et al. (1975) made similar observations of Starlings in Oregon, indicating that usually the earlier a bird leaves the roost the farther it travels to feed.

Grackles moved fairly directly toward their MDAR on 15 of the 21 mornings that we were able to follow them, but followed indirect routes the other 6 mornings, traveling many extra kilometers before reaching their

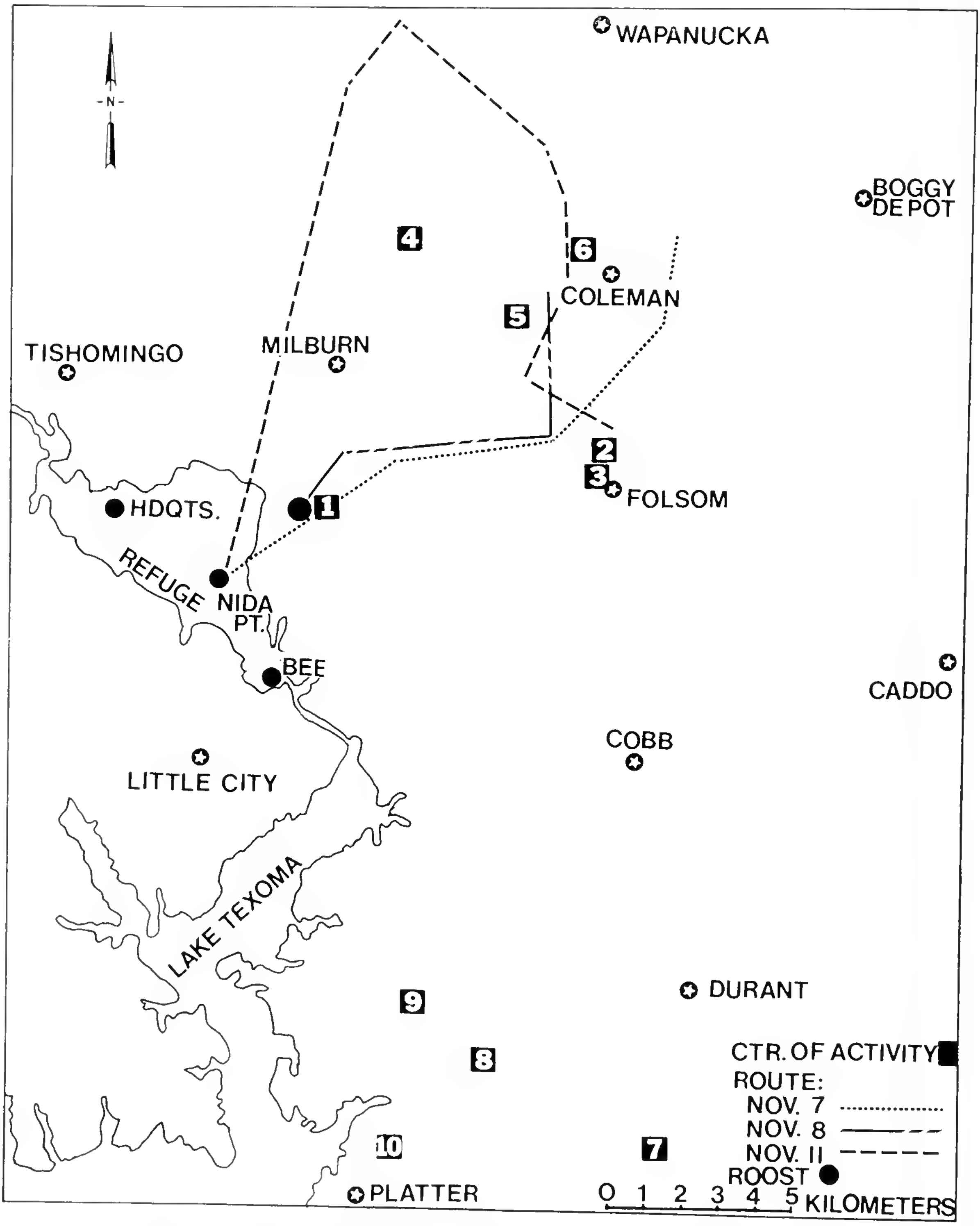

FIG. 1. Routes from the roost to the MDAR for bird 5 on 3 days, and the location of the centers of activity for bird 2. Numbers within the center of activity symbol refer to the number of days after instrumentation.

destinations. The 3 routes in Fig. 1 show the variation in the movement patterns of 1 bird between a roost and a MDAR. On 11 November this bird traveled at least 47 km before establishing a MDAR that was 17.5 km from its roost. Another bird established a MDAR 39.3 km from its roost after traveling at least 68 km. Neither weather conditions nor roost switches appeared to cause the indirect movements. Perhaps they were the result of a search for new feeding areas, as distance between the center of activity and the preceding day's center of activity averaged 16.6 km on days of indirect movements, but only 5.5 km on days of direct movements. However, birds sometimes moved directly to new areas, and sometimes after indirect movement they ended up in an area previously visited.

On 21 bird-days when departure time was obtained, grackles left their MDARs an average of 55 min before sunset (range 33–124), tending to leave MDARs earlier on completely overcast days or when the MDAR was a greater distance from the roost. These findings agree with those from previous radio-telemetry work (Bray et al. 1975).

Instrumented birds did not always follow the same route when flying to a roost from an area visited on previous days, and there was no tendency to retrace the route used that morning. They frequently bypassed 1 of the 3 major roosts, after flying close to it, and continued on to another roost. Radio-equipped birds that were close to each other during the day did not always go to the same roost that evening.

The MDAR.—The azimuths and distances of centers of activity from the Nida Point roost are shown in Table 1. The MDARs of grackles remaining in the refuge area were scattered but somewhat clustered, with most birds having more than 1 cluster (Fig. 1). The subject bird in Fig. 1 spent 5 days in the area north and west of Folsom, then moved south to spend the next 4 days in the area north and east of Platter. The change in areas was not due to food supply or roost switches, but may be related to flock behavior (see "Flocks" section). The degree of scattering did not vary greatly. A 2-way analysis of variance indicated that there was no significant difference ($P > 0.05$) among birds in the distance of the center of activity from that of the preceding day. The distance between centers of activity on successive days averaged 11.9 km.

The distance of centers of activity from the previous night's roost averaged 23.5 km for birds that remained in the refuge area (Table 1). A 2-way analysis of variance showed at least 1 significant difference ($P < 0.05$) among birds in this paramcter. The maximum distance was 44.6 km.

The mean activity radius of MDARs averaged 1.9 km (SD 1.6, range 0.2–5.0 km) on 15 bird-days that birds were adequately monitored. The mean activity radius averaged 2.6 km on days of direct movement to the MDAR, but only 1.3 km on days of indirect movement, indicating a relationship between activity radius and route traveled between the roost and

TABLE 1

DAILY MOVEMENT DATA FOR COMMON GRACKLES RADIO-TRACKED IN OKLAHOMA

Bird number	Number days monitored[a]	Azimuth, Nida Point roost to center of activity (degrees)	Distance of center of activity from Nida Point roost (km)		Distance of center of activity from previous night's roost (km)		Distance of center of activity from previous day's center (km)		Home range (km²)
		Range	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	
Birds that roosted in the refuge area every night.									
1	6	44–162	10.5–21.4	15.0 ± 5.1	10.6–21.4	16.4 ± 4.0	0.8–28.0	12.2 ± 10.3	199
2	9	29–164	15.9–31.4	21.1 ± 5.3	15.9–31.4	22.9 ± 6.4	0.5–38.5	10.5 ± 11.4	316
3	8	141–322	11.1–28.5	23.7 ± 6.8	10.3–32.2	25.3 ± 7.7	1.0–39.6	11.6 ± 13.0	218
4	5	148–318	8.7–28.0	16.4 ± 8.0	3.7–32.5	13.4 ± 11.7	1.9–42.2	13.2 ± 16.6	158
5	6	58–171	15.8–29.9	23.7 ± 5.8	15.8–29.9	23.2 ± 5.6	4.0–43.5	17.5 ± 17.4	736
6	2	66–74	24.8–29.6	27.2 ± 3.4	23.3–24.8	24.1 ± 1.0	5.8–12.9	8.5 ± 5.0	—
7	3	123–136	35.7–44.6	39.9 ± 4.5	35.7–44.6	39.9 ± 4.5	9.0– 9.2	9.0 ± 0.2	—
All 7 birds	39	29–322	8.7–44.6	23.8 ± 8.2	3.7–44.6	23.5 ± 8.4	0.5–43.5	11.9 ± 2.9	325.4 ±[b] 236.5
Birds monitored in refuge area and after they migrated.									
8	4	57–117	18.2–45.7	31.9 ± 15.4	8.7–18.8	15.3 ± 5.6	0.8–35.1	14.6 ± 14.6	
9	4	111–133	23.8–65.2	52.6 ± 19.3	7.7–32.7	21.4 ± 12.7	3.1–41.2	17.7 ± 17.1	
10	3	79–132	18.5–62.6	47.3 ± 24.9	5.1–58.1	27.2 ± 27.5	0.8–53.4	18.7 ± 30.1	
All 3 birds	11	57–133	18.2–65.2	43.9 ± 10.8	5.1–58.1	21.2 ± 6.0	0.8–53.4	17.1 ± 2.1	

[a] After the 1-day recovery period.

[b] Mean ± the standard deviation.

the MDAR. No relationships of mean activity radius to other factors were apparent. Precipitation had an effect with Starlings in Oregon (Bray et al. 1975).

Home range.—Home ranges averaged 325.4 km^2 for the 5 birds that remained in the refuge area and were monitored for 5 days or more (Table 1). The home ranges of 3 grackles are mapped in Fig. 2. Despite the relatively short length of the tracking periods, home range sizes were quite large because birds often visited new areas and were constantly changing the location of their MDARs. Home range size was increased greatly by the indirect routes that grackles often took while flying between the roost and the MDAR. By connecting the extreme outermost fixes of home ranges, we calculated a minimum area of 1990 km^2 used by the grackle population roosting at the 3 major roosts.

Flocks.—Telemetry and visual observations together showed the instability, within a day and between days, of large flocks of grackles. To illustrate, on 11 November 1971, birds 2 and 3 left the Headquarters roost 14 min apart and returned there in the evening, passing Little City (Fig. 2) 7 min apart. During the day they were in the same flock 3 times (09:00, 10:55, 15:00), but each time they separated with flocks that moved 1.1 to 2.3 km apart. Both birds were monitored for 2 more days but were never together again. While in their MDAR, instrumented birds were usually seen with more than 1000 grackles, the maximum being 70,000. Flock size was not consistent throughout the day, nor was there a discernible pattern of buildup or reduction except at staging time when flock size usually increased.

These findings are similar to those for the Red-winged Blackbird. From retraps of banded red-wings, Packard (1936) found that the makeup of flocks appeared to change continually, as individuals frequently shifted flocks. Smith and Bird (1969:44) suggested that "A blackbird flock appears to be an open community that can be added to or subtracted from readily."

Migration.—Six of the 10 birds migrated while their transmitters were operating. Five of them migrated ahead of or during cold fronts. This behavior was typical, for the grackle population at the 3 major roosts dropped drastically as each cold front moved through. We noticed no changes in the activities of the instrumented birds that would indicate they were about to migrate.

One grackle migrated when it left the Bee roost at 06:47 and flew 58.7 km southeast to near Ivanhoe, Texas. Later that day the bird moved northeast 13.7 km to near Elwood, Texas. Its center of activity was 53.4 km from

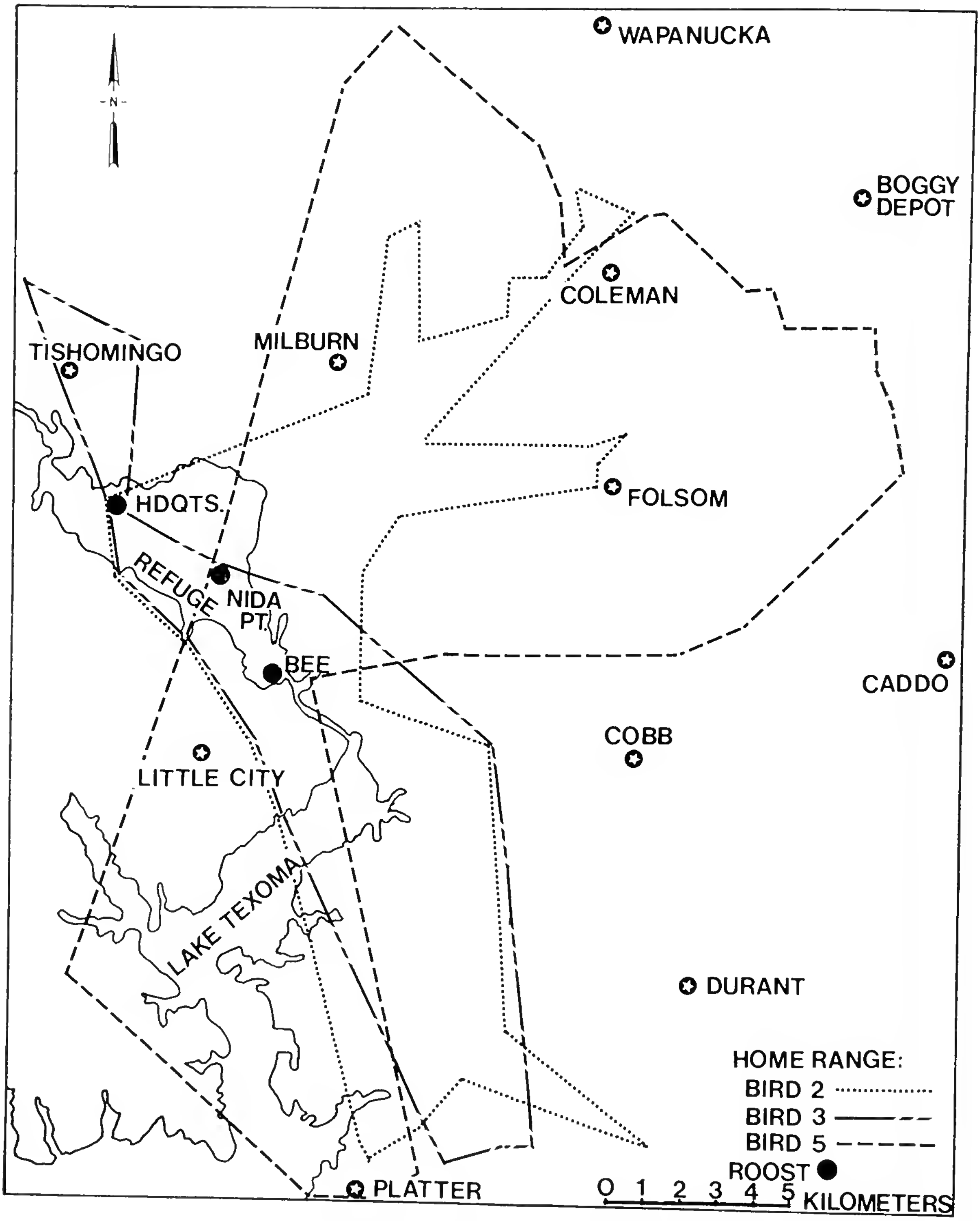

FIG. 2. Home ranges of 3 radio-equipped Common Grackles.

that of the previous day. Two other grackles evidently migrated in the morning also, but were not located after they left the refuge area.

The other 3 grackles migrated after they left their MDARs from 44 to 62 min before sunset and flew south. Two of these birds were on MDARs northeast of the refuge (near Boggy Depot and Folsom, Fig. 2) and the other was southeast of the refuge (near Cobb). We were unable to keep up with the birds, so we did not locate their roosts that evening. Two of the birds were located the next day, one near Bokchito, Oklahoma, the other near Elwood, Texas (centers of activity were 35.1 and 41.2 km, respectively, from those of the previous day).

These movements were characteristically like those of "near migrants," i.e., those having a prolonged migration wherein migration thrusts are interspersed with feeding pauses of 4–10 days (Blyumental' 1973). However, the 35–53 km movements were much shorter than the 200 km or greater distance of thrusts to which Blyumental' referred.

Management implications.—Within MDARs, 31% of 251 fixes on instrumented grackles were in oak forests, 29% in harvested peanut fields, 24% in pastures and only 6% in unharvested peanut fields. Moreover, only 3 of 58 peanut fields used by these grackles were unharvested. The heavy use of harvested fields was due to the abundance of waste peanuts in many fields (> 70%) that were harvested before or during the tracking periods, and because many farmers used bird frightening devices in unharvested fields. Peanut growers could lower bird pressure on unharvested peanut fields and other maturing crops by delaying tillage of harvested fields until all waste peanuts are eaten, or until all grackles have migrated.

There were only 2 instances when a radio-equipped grackle revisited a peanut field it had used on a previous day. We may infer that it would be easier for growers to frighten birds from unharvested fields if the birds did not become habituated to those fields. However, it also means that for any given field, continuous control efforts would be needed. A chemical fright-producing agent as referred to by Mott et al. (1972) would work most effectively if all peanut growers in an area used it, so that depredating birds would associate peanuts (rather than a particular field) with the control agent.

The lack of feeding site fidelity observed in our study was in contrast to Meanley's (1971:24) finding that some color-marked Red-winged Blackbirds returned daily to feed in the same part of a ripening ricefield in Arkansas. He indicated other blackbirds (including Common Grackles) also exhibited this behavior.

SUMMARY

Ten Common Grackles captured in the northern part of Lake Texoma, Oklahoma, were radio-equipped and monitored for 63 bird-days in November during the peanut damage season. This paper emphasizes those findings that cannot be obtained from visual observations alone.

The birds used 3 major marsh roosts on 38 of 40 bird-nights that they roosted in that area, but they switched roosts 10 times. Three graekles were located in 5 different roosts after they migrated. The distance between the 5 roosts and the previous night's roost varied from 9.3 to 52.8 km.

The distance of center of activity of the major diurnal activity range (MDAR) from the previous night's roost averaged 23.5 km for birds that remained in the refuge area. Distances between centers of activity on successive days averaged 11.9 km, but these centers tended to be clustered. The mean activity radius of MDARs averaged 1.9 km. Home ranges averaged 325.4 km^2. The minimum area used by the roosting population was calculated to be 1990 km^2.

While in their MDARs, instrumented grackles spent most of their time in oak forests, peanut fields (29% in harvested fields and 6% in unharvested), and pastures. They used 58 peanut fields (55 harvested and 3 unharvested), but individuals rarely revisited a field they had used on a previous day. The daily and day-to-day composition of large flocks of grackles was unstable.

Of 6 grackles that migrated, 5 moved out ahead of or during cold fronts. Three migrated in the morning after leaving the roost and 3 migrated from their MDAR in the late afternoon. Migration thrusts ranged from 35 to 53 km.

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SEVERE WINTER WEATHER AND BIRD POPULATIONS IN SOUTHERN ILLINOIS

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In 1973 we initiated a comparative study of bird populations in 5 mature upland and in 10 mature bottomland forests in southern Illinois, censusing the same tracts winter and summer. We censused the study areas in the winters of 1973–74, 1974–75, 1975–76, and had finished about one-half of the census in 1976–77 when heavy snow (for the region) with extreme cold covered the area on 7 January. Conditions were so severe that police stopped highway travel for several days, and we were forced to curtail our censusing. We did not resume censusing until 3 February, from which date to 18 February we completed our usual census routes and repeated all that we had done earlier in the season.

The comparison between our early and late censuses within the 1977 season and with other years provides an interesting picture of responses of bird populations to exceptional weather.

METHODS

Our strip censuses were made by 2 observers walking at a fairly constant rate (average, 2.4 km per h), counting birds that occurred within a 27.5 m-wide transect of the habitat (Graber and Graber 1963). To reduce variability in the counts, we used marked routes in relatively large tracts, censused within a limited time period daily and seasonally, and censused only when weather permitted suitable visibility. Total area of individual tracts censused varied from 109 ha to over 500 ha. The total area of census transects in bottomland forest averaged 189.4 ha per winter, with the transect area of separate tracts averaging 19.8 ha. Upland forest transects each winter averaged 101.6 ha, with the transects in separate tracts averaging 19.8 ha. All censuses were made between 08:00 and 16:00 CST, and between 26 December and 1 February, except in 1977 when the repeat censuses extended to 18 February. In addition to the forest censuses, urban residential habitat (77.3 ha) was censused in 3 towns—Anna, Carmi, and Mt. Vernon—in the winter of 1975–76. In the winter of 1976–77 we had time to census only 1 town (Metropolis), but this town was censused both before and after the severe weather. The length of our census transects in all habitats totalled 380 km in the winter of 1976–77.

The bottomland forests we censused occupied the floodplain and the first level above, along larger streams in southern Illinois (Fig. 1, nos. 1–4, 6, 8, 10, 11, 13, 15). The trees reached a maximum diameter (DBH) of 122 cm, and there were from 1 to 8 large (over 56 cm DBH) trees per ha. The upland forests censused occupied the hilltops and ravines and had trees that reached a maximum diameter of 127 cm, with 1 to 9 large trees per ha. Genera comprising 85% (based on importance, see Lindsey et al. 1958) of the bottomland forests were *Quercus*, *Carya*, *Acer*, *Celtis*, *Ulmus*, *Fraxinus*, and *Liquidambar*. The same genera, plus 2 others—*Liriodendron* and *Sassafras*—made up 85% of the trees in the

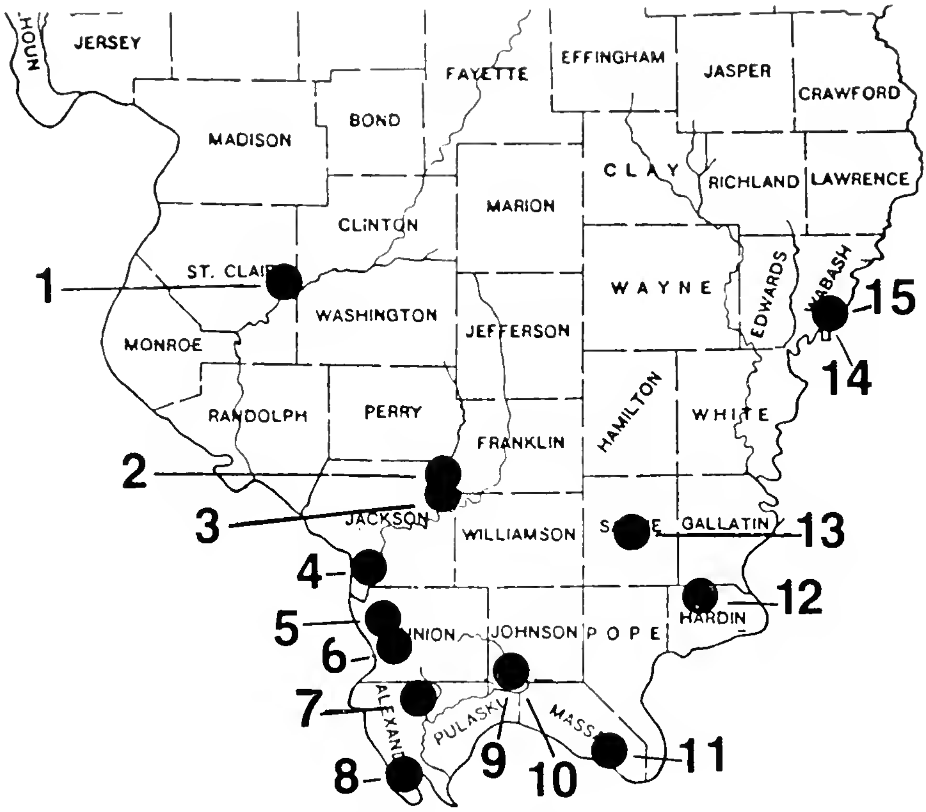

FIG. 1. Location of forest census areas in Southern Illinois. 1—Jim's Pond on the Kaskaskia River; 2, 3—Campbell Lake, Snyder Lake on the Little Muddy River; 4—Oakwood Bottoms on the Big Muddy River; 5—Pine Hills-LaRue Ecological Area; 6—Union County Conservation Area; 7—Possom Trot Trail near Elco; 8—Horseshoe Lake Island Nature Preserve; 9, 10—Heron Pond Nature Preserve, upland and bottomland on the Cache River; 11—Ft. Massac State Park on the Ohio River; 12—Kaskaskia Experimental Forest; 13—Barnes and Evans' tract on the Middle Fork of the Saline River; 14, 15—Beall Woods, upland and bottomland on the Wabash River.

upland forests censused. The difference between the uplands and bottomlands lay chiefly in topography and in the species of woody plants in the 2 habitats.

We have discussed only species encountered in the transects in 1976–77 and only those (woodpeckers and passerines) whose range of activity allows reasonable estimate of their numbers in the censused acreage by the procedure used. Other species occurring within the transects were Turkey (*Cathartes aura*) and Black (*Coragyps atrata*) vultures, Red-tailed (*Buteo jamaicensis*) and Red-shouldered (*B. lineatus*) hawks, Rock (*Columba livia*) and Mourning (*Zenaida macroura*) doves, and Great Horned (*Bubo virginianus*) and Barred (*Strix varia*) owls. We did not make systematic searches for dead birds but identified dead specimens we happened to see during the censuses.

RESULTS

The severity of the winter 1976–77 can be seen by comparing the climatological records of the previous 3 winters with those of 1976–77 (Table 1). The stations listed in Table 1 represent the longitudinal and

TABLE 1

TEMPERATURE AND DEPTH AND DURATION OF SNOW COVER AT 3 STATIONS IN SOUTHERN ILLINOIS DURING DECEMBER–FEBRUARY 1973–1977 (U.S. ENVIRONMENTAL SERVICE DATA 1973–1977)

		Nashville			Rosiclaire			Cairo		
Measurement	Year	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.
Maximum depth of snow on ground (cm)	1973	23			10			8		
	1974	8	5	10	2	2	0	0	T[1]	T
	1975	15	2	8	2	T	T	2	T	T
	1976	8	8	5	2	2	8	2	2	8
	1977		41	28		23	10		15	2
Number of days with 1.3 cm or more of snow on the ground	1973	8			4			2		
	1974	–	14	0	0	3	0	0	0	1
	1975	4	–	1	0	0	1	0	0	0
	1976	0	4	5	0	1	2	0	1	2
	1977		31	9		27	6		26	2
Lowest temperature for month (°C)	1973	–18.3			–16.7			–13.9		
	1974	–8.9	–19.4	–12.8	–8.3	–15.0	–10.0	–6.7	–13.9	–13.9
	1975	–13.3	–12.2	–15.5	–11.7	–12.2	–12.2	–10.5	–10.0	–10.0
	1976	–20.0	–19.4	–15.0	–20.5	–18.9	–13.9	–17.2	–15.0	–8.3
	1977		–27.8	–17.8		–26.7	–16.1		–18.3	–12.2
Average temperature for month (°C)	1973	0.5			2.2			2.9		
	1974	2.3	0.7	3.4	3.7	3.7	4.7	3.9	3.3	5.2
	1975	2.4	1.9	1.6	3.6	3.7	3.8	5.1	4.1	4.4
	1976	–1.1	–1.6	6.6	0.6	–0.3	7.7	2.1	1.6	9.5
	1977		–9.2	1.3		–7.1	2.0		–5.3	4.0

[1] Trace of snow.

latitudinal extent of all areas censused. There were very low temperatures and heavy snow cover that remained for an exceptionally long period for the region (over a month).

Overall, the bird population declined sharply during the severe weather, falling about 58% in bottomland and 66% in upland forest. By contrast there was a slight increase (9%) in the urban habitat (Table 2). Early in the winter, bird populations in both forest habitats were higher than average (bottomland, 1.4×; upland, 2.0×), but the urban habitat appeared to have lower numbers of birds than in 1975–76 (0.8×). These figures are important to understanding the population pressure on each habitat.

The decline during the winter was not uniform among species of birds. Of the 37 species in bottomland forest, 28 (73%) lost in numbers, 8 gained, and 1 remained the same (Table 2). Fourteen bottomland species lost over 50% of their early winter populations. Another 4 species of the bottomland each declined by over 40%. Of the 25 species in upland forest, 12 declined (48%) whereas 13 gained in numbers. Ten species in upland forest were each reduced by more than 50%. In urban residential habitat 7 species declined in numbers (37%) and 12 gained. Five species in this habitat lost as much as 50% of their populations.

Of the possible explanations for rather abrupt population declines, the most probable would seem to be emigration, local movement, and/or mortality. We do not believe that changing conspicuousness of birds was an important factor in the observed changes, except possibly in the case of the Pileated Woodpecker.

The reasons for changes in numbers of birds are difficult to prove, especially with unmarked populations. Only the Cedar Waxwing declined conspicuously in numbers by February 1977 without evidence of habitat change or mortality. We presumed this species to have emigrated from the area.

The majority of the observed population changes seemed to involve some shift in habitat use. Examples were the Downy Woodpecker, Red-headed Woodpecker, White-breasted Nuthatch, and Yellow-rumped Warbler, all of which appeared to have moved at least some of their population from bottomland to upland forest. Only the robin shifted from upland to bottomland forest. Crows and shrikes probably shifted from more open habitats to forest. The shrikes are particularly interesting as we have never encountered them in forest habitat before. A number of species—Red-bellied Woodpecker, Blue Jay, titmouse, chickadee, Mockingbird, robin, Starling, Purple Finch, junco, and White-throated Sparrow—showed evidence of population shift to urban residential habitat.

Some of the population decline definitely represented mortality, indicated by our finding of dead specimens on the snow. In other years we have rarely found dead birds while censusing; the method is ill-designed for finding them, as the observer's attention is focused away from his own proximity. Thus, the finding of any dead birds may be indicative of high mortality, and the fact that we found no dead of some species should not be construed as an absence of mortality. All specimens we found were on top of the snow. Birds that died during the blizzard would have been covered. In February 1977 we found the remains of 6 flickers, 1 Pileated Woodpecker, 2 immature and 1 adult Red-headed Woodpeckers, 2 Downy Woodpeckers, 4 Blue Jays, 4 titmice, 2 Carolina Wrens, 1 Brown Thrasher, 4 robins, 2 bluebirds, 2 kinglets, 2 Yellow-rumped Warblers, 3 red-wings, 9 grackles, 3 Cardinals, 1 Purple Finch, 4 towhees, 6 juncos, 1 Tree Sparrow, and 3 white-throats. Besides carcasses we found numerous flight feathers, especially from flickers and immature Red-headed Woodpeckers.

TABLE 2

WINTER BIRDS PER 40.5 HA IN MATURE BOTTOMLAND AND UPLAND FOREST AND URBAN RESIDENTIAL HABITAT IN SOUTHERN ILLINOIS BEFORE AND AFTER SEVERE WINTER WEATHER IN JANUARY 1977, PLUS THE AVERAGE DENSITY FOR THE PRECEDING 3 WINTERS (1974–76)

	Bottomland forest				Upland forest				Urban residential			
	1977		1977 %	3-year	1977		1977 %	3-year	1977		1977 %	1975–
Species	Dec.–Jan.	Feb.	change	mean	Dec.–Jan.	Feb.	change	mean	Dec.–Jan.	Feb.	change	1976
Yellow-shafted Flicker (*Colaptes a. auratus*)	11.9	4.6	–61.3	5.4	1.1	0.9	–18.2	2.6	5.1	3.2	–37.3	1.0
Pileated Woodpecker (*Dryocopus pileatus*)	0	3.6	+	0.9	0	0.4	+	0.2	0	1.6	+	0.5
Red-bellied Woodpecker (*Melanerpes carolinus*)	8.9	8.7	–2.2	9.4	15.0	6.4	–57.3	6.5	1.3	4.7	+261.5	5.2
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	79.6	47.5	–40.3	34.2	3.2	19.7	+515.6	8.4	0	0	0	0.5
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3.0	0.8	–73.3	1.6	0	0.4	+	0.4	3.8	1.6	–57.9	1.6
Hairy Woodpecker (*Picoides villosus*)	1.7	1.7	0	0.9	0	0.4	+	0.9	0	0	0	2.1
Downy Woodpecker (*Picoides pubescens*)	15.3	8.2	–46.4	13.7	2.1	3.8	+80.9	5.6	3.8	0	–100	3.7
Blue Jay (*Cyanocitta cristata*)	15.3	10.8	–29.4	11.6	9.7	9.8	+0.1	5.1	17.9	31.6	+76.5	31.9
Common Crow (*Corvus brachyrhynchos*)	1.3	3.2	+146	2.7	0	5.6	+	0.1	0	0	0	0
Carolina Chickadee (*Parus carolinensis*)	24.3	11.6	–52.3	14.6	8.6	9.4	+9.3	5.0	0	1.6	+	4.2

TABLE 2 (continued)

	Bottomland forest				Upland forest				Urban residential			
	1977		1977 % change	3-year mean	1977		1977 % change	3-year mean	1977		1977 % change	1975–1976
Species	Dec.–Jan.	Feb.			Dec.–Jan.	Feb.			Dec.–Jan.	Feb.		
Eastern Tufted Titmouse (*Parus b. bicolor*)	24.7	12.5	-49.4	27.3	12.9	13.7	+6.2	13.8	0	1.6	+	0.5
White-breasted Nuthatch (*Sitta carolinensis*)	3.0	1.7	-43.3	2.3	0	2.1	+	4.6	0	0	0	0
Brown Creeper (*Certhia familiaris*)	3.8	3.2	-15.8	3.0	2.1	1.3	-38.1	1.1	0	0	0	0
Winter Wren (*Troglodytes troglodytes*)	0.8	0	-100	1.7	0	0	0	0	0	0	0	0
Carolina Wren (*Thyrothorus ludovicianus*)	4.3	0	-100	4.0	0	0	0	1.8	0	0	0	2.6
Mockingbird (*Mimus polyglottos*)	0	0	0	0.1	0	0	0	0	1.3	11.1	+753.8	5.7
Brown Thrasher (*Toxostoma rufum*)	3.8	0.6	-84.2	0.6	0	0	0	0	0	0	0	1.0
American Robin (*Turdus migratorius*)	10.6	14.8	+40	11.2	61.3	6.0	-90.2	20.9	0	14.2	+	12.5
Hermit Thrush (*Catharus guttatus*)	0	0	0	1.0	3.2	0	-100	0.5	0	0	0	0
Eastern Bluebird (*Sialia sialis*)	2.5	0.4	-84	4.2	8.6	0.9	-89.5	2.2	0	0	0	0
Golden-crown Kinglet (*Regulus satrapa*)	5.5	0	-100	7.4	4.3	0	-100	5.4	0	0	0	0

TABLE 2 (continued)

Species	Bottomland forest				Upland forest				Urban residential			
	1977		1977 % change	3-year mean	1977		1977 % change	3-year mean	1977		1977 % change	1975–1976
	Dec.–Jan.	Feb.			Dec.–Jan.	Feb.			Dec.–Jan.	Feb.		
Ruby-crowned Kinglet (*Regulus calendula*)	1.3	0	–100	0.8	0	0	0	0.4	1.3	0	–100	0
Cedar Waxwing (*Bombycilla cedrorum*)	12.8	0	–100	0	78.5	0	–100	0	0	0	0	0
Loggerhead Shrike (*Lanius ludovicianus*)	0.8	0.2	–75	0	0	0.4	+	0	0	0	0	0
Starling (*Sturnus vulgaris*)	2.1	0	–100	3.9	9.7	0	–100	0.5	506.0	650.1	+28.5	688.3
Yellow-rumped Warbler (*Dendroica c. coronata*)	6.8	0.6	–91.2	4.6	3.2	5.1	+59.4	1.4	0	0	0	1.0
House Sparrow (*Passer domesticus*)	0	0	0	0	0	0	0	0	198.6	204.0	+2.7	302.1
Red-winged Blackbird (*Agelaius phoeniceus*)	11.9	10.6	–10.9	13.8*	0	0	0	0	0	0	0	0
Rusty Blackbird (*Euphagus carolinus*)	0.8	0.2	–75	11.4	0	0	0	0	0	0	0	0
Common Grackle (*Quiscalus quiscula*)	25.5	20.7	–18.9	28.2*	0	0	0	2.2	161.4	53.8	–66.7	2.6
Cardinal (*Cardinalis cardinalis*)	22.6	5.9	–73.9	23.8	6.4	3.0	–53.1	7.3	38.4	38.0	–1.0	30.8

* 2-year average (1974–75 and 1975–76).

TABLE 2 (continued)

Species	Bottomland forest				Upland forest				Urban residential			
	1977		1977 % change	3-year mean	1977		1977 % change	3-year mean	1977		1977 % change	1975–1976
	Dec.–Jan.	Feb.			Dec.–Jan.	Feb.			Dec.–Jan.	Feb.		
Purple Finch (*Carpodacus purpureus*)	0.4	0.2	-50	1.6	8.6	0	-100	0.3	1.3	9.5	+630.8	0
American Goldfinch (*Carduelis tristis*)	4.7	7.8	+66	13.0	0	0.4	+	1.0	0	0	0	3.7
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	17.4	2.1	-87.9	1.9	0	0	0	0.2	0	0	0	0
Slate-colored Junco (*Junco h. hyemalis*)	25.5	4.4	-82.8	25.4	37.6	5.1	-86.4	34.1	30.7	33.2	+8.1	74.2
Tree Sparrow (*Spizella arborea*)	0	1.7	+	7.4	0	0	0	1.9	0	0	0	0
Field Sparrow (*Spizella pusilla*)	3.0	0	-100	0.7	0	0	0	1.0	3.8	0	-100	7.8
White-throated Sparrow (*Zonotrichia albicollis*)	99.6	0.3	-99.7	29.4	0	0	0	0.3	0	4.7	+	0.5
Swamp Sparrow (*Melospiza georgiana*)	0	0.2	+	3.4	0	0	0	0	0	0	0	0
Song Sparrow (*Melospiza melodia*)	0	0.4	+	2.7	0	0	0	0.2	0	0	0	7.3
Total birds per 40.5 ha	455.5	189.2	-58.5	329.8	276.1	94.8	-65.7	135.9	974.7	1064.5	+9.2	1191.3
Total ha censused	95.1	191.6		188.5	37.6	94.5		104.1	31.6	25.6		77.4

In the case of the Hermit Thrush, the 2 wrens, the 2 kinglets, and the Field Sparrow we believe there was 100% mortality. There was also very high mortality in the flicker, Brown Thrasher, bluebird, Cardinal, towhee, junco, and White-throated Sparrow. In addition, we suspect that there was more mortality than might be expected of Red-bellied Woodpeckers, sapsuckers, and Brown Creepers. The expected winter mortality is unknown and undoubtedly varies from species to species. Lack (1966) recorded winter-to-spring mortality of 31–75% in the Great Tit (*Parus major*) in different years, with the highest mortality in a severe winter. It should be remembered that the losses described in this paper represent only 1 month and not the whole winter season.

DISCUSSION

Interpretation of changes in densities of populations as mobile as birds is particularly difficult, and studies that deal with single habitats may be especially misleading. Our study, which included only arboreal habitats, indicated a decline of 61% in the flicker population in bottomland forest, an 18% loss in upland forest, and a 37% loss in residential habitat. The available evidence (large numbers of dead specimens) suggests that these losses represent mortality. Our earlier studies on Illinois populations (Graber and Graber 1963) indicate that arboreal habitats hold only about 3% of the total flicker population in southern Illinois in winter. We might assume that mortality in more open habitats was at least as great, but the problem is more complicated than that, as some populations moved from more open habitats to forest, and what we construed as 61, 18, or 37% mortality may have been much greater, because our before-and-after density figures do not account for birds that may have moved into the habitat and died in the period between the counts.

In assessing population losses and gains, one must also take into account the available areas of habitats. Our study areas were chosen for maturity and large area size and are not strictly representative of southern Illinois forests in general, but populations in other forests were probably at least as vulnerable as those we observed. We have estimated that there are about 218,535 ha of bottomland forest, 517,321 ha of upland forest, and 122,865 ha of residential habitat in southern Illinois (Graber and Graber 1976). At the observed densities for these habitats we could estimate that there were, for example, about 241,400 Carolina Chickadees before the severe weather and 187,000 after (including about 4900 in urban habitat), a net loss of about 22% for the month. The great loss in bottomland forest was somewhat counterbalanced by smaller increases in upland forest, because the area of upland forest is more than twice as great as the bottomland. If we assume the observed density changes represent emigration, the possibility of mortality is still not eliminated. Conditions as bad or worse than those that prevailed in southern Illinois existed several hundred km in all directions. If a bird cannot survive where it knows the resources, moving to an unknown and probably already occupied area is not likely to improve the situation and involves an energy cost that increases with distance.

We believe that most of the observed density changes that were not the result of mortality represented only local movements by birds in search of special food situations. Thus, Yellow-rumped Warblers virtually disappeared from bottomland forests (their preferred winter habitat) and became numerous in certain upland forests that had an abundance of poison ivy (*Rhus radicans*) fruits. Early in the winter we found flocks of robins feeding on the fruit of shining sumac (*R. copallina*) and greenbrier (*Smilax bona-nox*) in upland forests. In February the uplands were bare of these fruits and robin flocks were congregating to feed on persimmons (*Diospyros virginiana*) in bottomland forests. A late frost in May 1976 retarded the development of persimmons so that these fruits remained on the branches and were thus available when snow covered the ground. The same freeze also retarded the development of acorns in the upland forests so that many acorns were also still on the branches in February; they were probably the reason for the shift of Red-headed Woodpeckers from the bottomland forests to the upland.

Interspecific competition is probably accentuated with severe weather. Red-headed and Red-bellied woodpeckers are both mast feeders, and their populations show a consistent inverse relationship in Illinois in winter (Graber et al. 1977). In southern Illinois red-head populations are correlated positively with alternate-year highs in the acorn crop. The highs in recent decades have occurred in (January) the odd-numeral years, and 1977 was typically high with an exceptionally large population of red-heads. The red-head population is usually concentrated in bottomland forest. Red-bellies also show a preference for bottomland forest, but in years with high densities of Red-headed Woodpeckers, red-bellies are apparently unable to compete and move to upland forest, as they did in the winter of 1976–77 (Table 2). When snow covered the mast crop, red-heads moved to those upland areas where acorns remained on the trees. This move probably saved much of the red-head population but may have increased mortality of red-bellies, which, overall, lost more than 40% of their population.

A notable pattern in the data was the similarity of population changes in related species. For example, parids declined at similar rates in bottomland forest while increasing at similar rates in upland forest and urban habitat:

wrens and kinglets showed a total loss; and thrushes all lost heavily in upland forest. The observation implies consistent responses to stress by congeners among a wide range of species and perhaps a tendency to compete for the same resources. Population shifts between habitats by a species were invariably from habitats with high population density to those with lower density.

Certain species seem to be especially vulnerable to severe winter weather and have a history of population crashes. Included here are most of the species in which we observed a 100% decline. Population declines of the Carolina Wren in winter have been discussed by Bent (1948) and James (1961), and of bluebirds and Hermit Thrushes by James (1959, 1960, 1961, 1962). Bent (1949) mentioned possible mortality of Golden-crowned Kinglets in severe winters but not of Ruby-crowned Kinglets.

The disadvantage of heavy snow cover to ground foragers is evident, as 9 of the 11 species that suffered declines above 80% are ground foragers (e.g., Brown Thrasher, Winter Wren, towhee, junco).

Small size was also a great disadvantage (Fig. 2), with kinglets being particularly vulnerable and the only aboveground (arboreal) foragers to show a total loss.

Within a species, the inexperienced immature birds, and possibly also the aged and infirm, suffered the greatest losses. Two of the 3 Red-head specimens we found were immatures, and, in addition, we found a number of immature tertials from red-heads that may have died, though the feathers could also have been molted. Increased mortality of immatures in severe weather has been observed in the Great Tit by Lack (1966).

Birds near the northern limits of their winter range probably suffer the greatest losses when a severe winter occurs. Southern Illinois is near the northern limit of regular winter occurrence for some of the species that suffered high losses (e.g., Brown Thrasher, Hermit Thrush, Ruby-crowned Kinglet, Yellow-rumped Warbler).

Some birds survived the severe weather because of food provided by man. Bird feeders and special plantings in town were part of the reason bird populations increased in urban habitat (e.g., an 8-fold increase in Mockingbirds). Some ground foragers that survived (white-throats and juncos are examples), survived mainly in the urban habitat, and urban Cardinals apparently survived better than those in the natural habitats (Table 2). The only Swamp Sparrows we found after the blizzard were in bottomland woods near a large cattle-feeding station, where food in the form of silage, grain, and grass seed from hay was available.

Certain of our observations appear to exemplify an important biological principle—that mortality in times of crisis is directly proportional to what

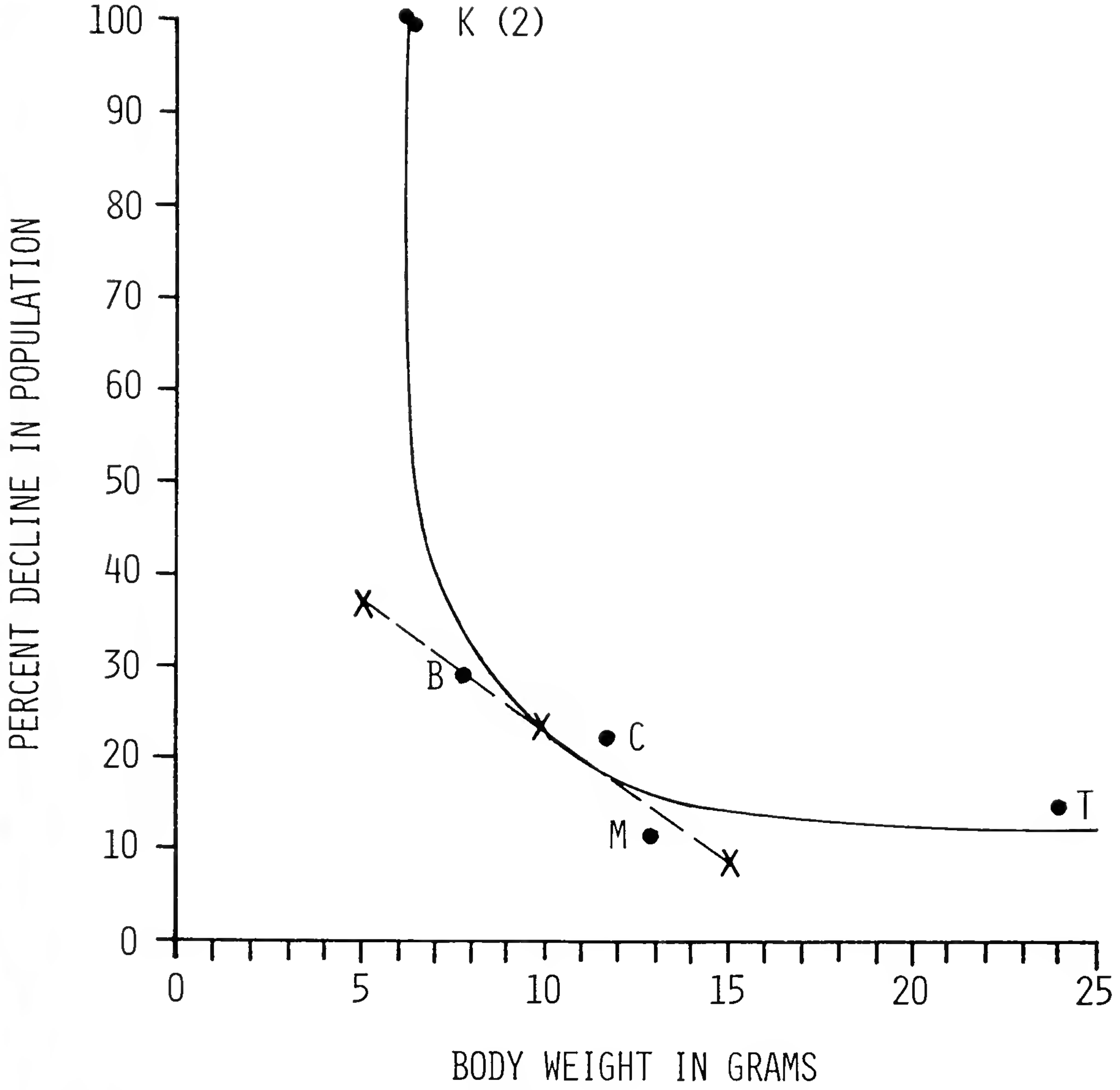

FIG. 2. Relationship between population loss and body weight of smaller species censused. Only arboreal foragers are included, as follows: K (2)—Golden-crowned and Ruby-crowned kinglets; B—Brown Creeper; C—Carolina Chickadee; M—Yellow-rumped Warbler; T—Tufted Titmouse. Weights are averages for 2 or more winter specimens. Dashed line represents calculated regression of population loss on weight for the 3 middle-range species ($r = 0.916$). The curve was estimated by eye.

could be called population pressure. A simple expression of that pressure is the total number of animals, or more precisely the biomass, and the variety of species, which, in effect, projects the influence of the mass. Bottomland forest characteristically supports more birds and more species than upland, in both respects absorbing more pressure on its resources per unit of area. Even lacking precise knowledge of what all the resources are, we can still presume that for bird populations at least, bottomland forest has more resources to exploit than upland, because of the bottomland's consistently higher, more varied population. For the fauna considered here, respective figures for the 3-year counts of species and the 3-year average of numbers of birds per 40.5 ha (100 acres) are: bottomland forest—37 species, 330 birds; upland forest—31 species, 136 birds. These average figures may represent about what the 2 habitats can support in winter over the years (that is, carrying capacity) for the usual range of conditions—weather, food supplies, and other basic needs. With the extraordinary climatic conditions of January 1977 closing off some of the (especially ground) resources, and at the same time increasing demand, not even the "usual" populations could have been sustained. We might assume that bottomland, having the most to lose (the highest population pressure), would lose more population than upland, but examination of the data (Table 2) reveals that bottomland forest lost about 58% and upland forest 66% of their populations, respectively. The losses are not related just to population pressure but to the amount of that pressure in relation to the carrying capacity of the habitat. Before the severe weather set in, bottomland with 455 birds had 38% more population than its (average) carrying capacity, whereas upland with 276 birds had 102% more than its capacity and consequently lost more. The data for urban habitat further substantiate the "mortality"-carrying capacity relationship. Early in winter the urban habitat (a consistently high-density habitat) had 975 birds per 40.5 ha, a number 18% below the capacity for the habitat, and in contrast to both the natural habitats, urban habitat actually gained (9%) in population during the winter.

What is true of the population in general is also true of the individual species. Considering the number of variable factors that affect the rate of population decline in different species during an adverse winter, it is remarkable that any single factor, such as population density, would show correlation with the decline. Yet the relationship between high population and high loss is so pronounced that a significant correlation ($r = 0.882$, Fig. 2) shows through the large specific differences in susceptibility, size, food habits, and similar factors. The graph was constructed by averaging the percentage losses of species falling in different categories of abundance.

The greater the number of birds of a species above the 3-year winter average, the greater the loss in both upland and bottomland forests (Fig. 3) during the winter of 1976–77. The Tufted Titmouse had 0.9× the average in early winter and its numbers declined 49% by February. The Brown Thrasher had 6.3× more than average and its losses were 89.5%. This relationship between abundance and amount of decline in numbers suggests that there is a limit to the number of birds of a species that can expect to obtain a survival level of sustenance in a given habitat. When numbers

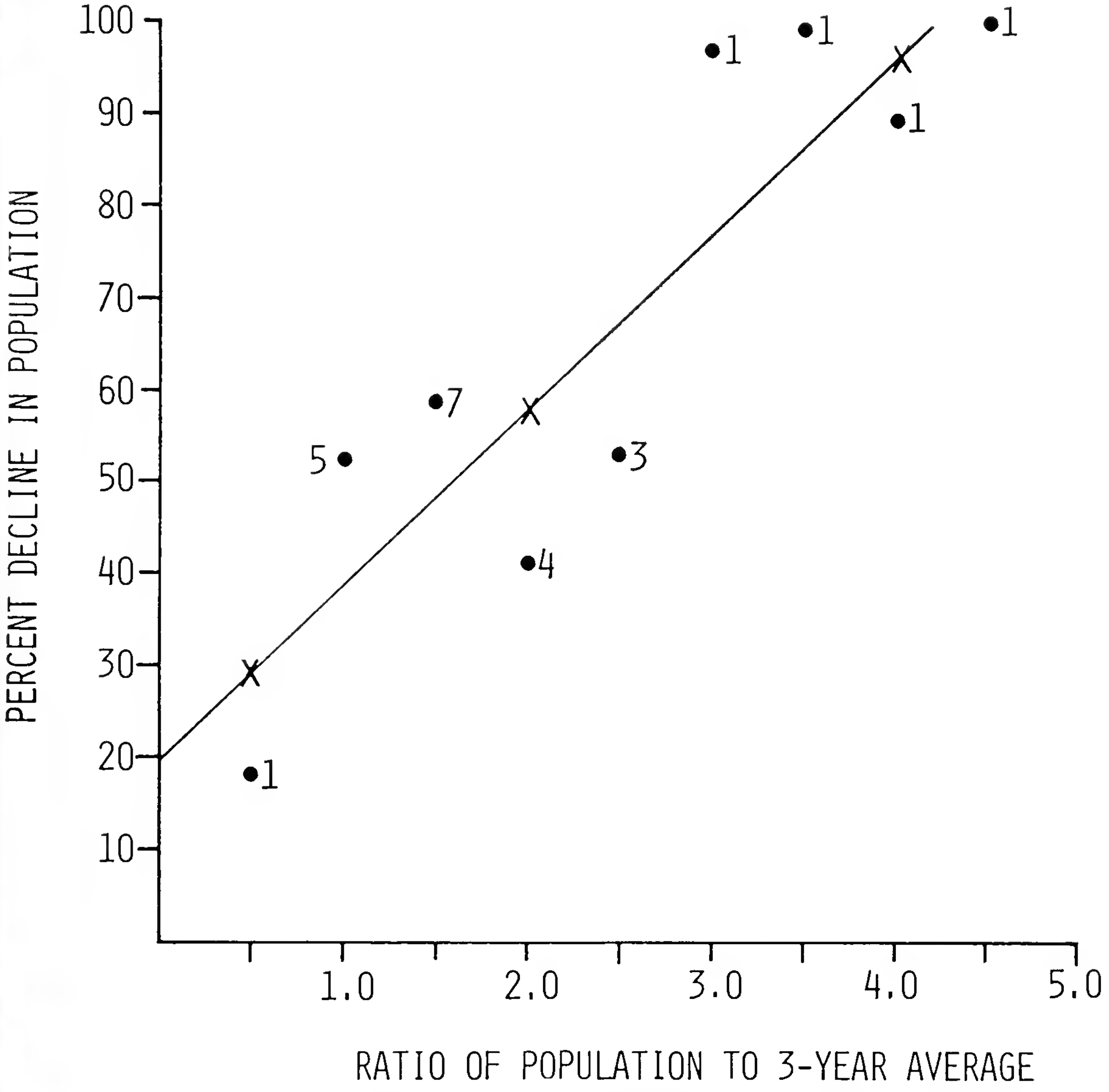

FIG. 3. Relationship of population decline in species of forest birds to their abundance in early winter, expressed as a ratio of the average winter population in the 3 preceding years (that is, 1.0 = average, 2.0 = twice the average). The numerals beside the points indicate the number of species represented by the point. Graph line is the calculated regression of population density on population loss.

exceed this level, mortality, dispersal, or both, reduce the surplus to sustainable populations. Given the initial population, the decline is predictable—the larger the population above carrying capacity, the greater the decline.

Bird populations are made up of individuals whose range of structure and behavior allows for maximum exploitation of resources and rapid adaptation to changing climatic conditions. Mild winter weather encourages the segment of a migratory species that is less inclined to migrate, whereas severe weather eliminates such birds. Mild winters may also allow northward expansion of species of southern origin, whereas inclement winters may result in a retraction of the range of such species. As Tramer (1974) has stated, winter range probably represents adaptation at the species population level to winter events that have a significant probability of occurring each winter in a given geographic region.

SUMMARY

A study was made of bird populations in 3 arboreal habitats—bottomland forests, upland forest, and urban, in southern Illinois, comparing the severe winter of 1976–77 with milder winters of the 3 previous years. Prolonged severe cold, and snow cover caused massive population shifts, and high mortality among several species of birds. Populations of certain species left their preferred winter habitats to use special food sources elsewhere. Mortality was particularly high among ground foragers, but mortality rate was also related to body size, smaller species showing the greatest decline. Closely related species showed very similar patterns of population change. Some populations survived better in urban habitat than in natural habitats probably because of food provided by humans. Population declines in a habitat were related to: (1) the initial winter population density, and (2) the carrying capacity of the habitat as expressed in the average population density for the habitat during more normal winters. The higher the population was above average, the greater the loss.

ACKNOWLEDGMENTS

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RED-SHOULDERED HAWK NESTING ECOLOGY AND BEHAVIOR

JOHN W. PORTNOY AND WENDELL E. DODGE

Wallace (1969), Brown (1971) and Henny (1972) suggest serious declines in Red-shouldered Hawk (*Buteo lineatus*) populations. Stewart (1949), and Henny et al. (1973) reported on intensive studies in Maryland, Craighead and Craighead (1956) in Michigan, and Wiley (1975) in California. None of these presented a detailed description of nesting behavior. This paper provides a detailed and quantitative description of behavior at 4 nests and presents various aspects of the ecology of a Red-shouldered Hawk population nesting in a reservoir watershed of central Massachusetts during 1973 and 1974.

STUDY AREA AND METHODS

Prescott Peninsula, averaging 3 km wide and extending, north to south, 16 km into Quabbin Reservoir of central Massachusetts, consists of about 5000 ha of hemlock (*Tsuga canadensis*)–white pine (*Pinus strobus*)–northern hardwoods forest. The hilly terrain ranges in elevation from 150 to 330 m. Eastern and western shores of the peninsula are steep, elevations normally increasing by 140 m from reservoir shoreline to 0.5 km inland. A nearly continuous series of streams and beaver impoundments characterizes the relatively flat central peninsula.

Upland vegetation consists mainly of red oak (*Quercus rubra*), black oak (*Q. velutina*), sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), and white pine. Wet areas are mainly forested with black birch (*Betula nigra*), yellow birch (*B. lutea*), and red maple (*Acer rubrum*). Small groves of hemlock occur in both uplands and lowlands. Forest coverage is continuous, except for unwooded beaver ponds and narrow roadways. Understory is lacking in most areas because of overbrowsing by white-tailed deer (*Odocoileus virginianus*). Ground cover includes *Vaccinium* spp. and ferns.

Other raptors that we observed nesting in the area included: Great-horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Red-tailed Hawk (*Buteo jamaicensis*), and Broad-winged Hawk (*Buteo platypterus*). Raptors observed occasionally during the breeding season, but not observed nesting, included: Turkey Vulture (*Cathartes aura*), Goshawk (*Accipiter gentilis*), Cooper's Hawk (*A. cooperii*), Sharp-shinned Hawk (*A. striatus*), Bald Eagle (*Haliaetus leucocephalus*), and American Kestrel (*Falco sparverius*).

Human activity on Quabbin Reservation is officially restricted to logging, road maintenance, and forestry and wildlife research; thus, human intrusions are infrequent.

Methods.—We located old raptor stick nests during the 1972–73 and 1973–74 winters by searching the peninsula on foot, and returned to these nests in March to determine activity. Courtship and territorial activity of Red-shouldered Hawks in March provided clues to locations of newly-constructed active nests. We recorded locations and activities of all hawks sighted in the study area during daily field visits from March through July.

Twelve nest sites used by breeding Red-shouldered Hawks during 1973 or 1974 were characterized, after young had fledged, by recording nest tree species, nest tree height, nest tree diameter at breast height (DBH), nest height, and slope aspect of the ground directly below the nest. We also described the forest cover type by identifying, measuring (DBH), and enumerating all trees (i.e. woody and at least 5 cm DBH) within 15 m of the nest tree.

We determined clutch-size at 9 nests by climbing nest trees during late incubation. We did not climb nest trees thereafter, but determined hatching dates by inspecting nests daily from adjacent trees. Fledging rate was ascertained at only 4 nests where blinds allowed frequent observations during the fledging period.

We collected regurgitated pellets in or under nests immediately after young had fledged, and identified prey from hair and bone remains. To watch specific feeding behaviors, we built blinds and spent 71 h observing sibling and parental interactions at 4 nests. Observations, of 3 to 14 h duration, began 10 days after eggs had hatched and continued at various times during the nestling period until young fledged. At the same time, we identified and counted prey items delivered by adults as a check on the verity of pellet analyses.

In addition, nesting behavior was recorded and timed at 4 nests in 1974, using time-lapse photorecorders. Two of these 4 nests were also monitored periodically by observers in blinds. Camera units consisted of Rollei SL-82 super 8 movie cameras (reference to commercial products does not imply endorsement by the U.S. Government) set for single frame exposure and exposed by use of a solenoid-activated mechanical trigger (Temple 1972) and an astable free-running multivibrator timing device (Fig. 1). We packaged camera and timing components in a water-proofed plywood box. A 6-volt storage battery provided power for the intervalometer circuitry and was separately housed with electrical leads routed through a hole in the housing. Each camera unit was bolted to an adjacent tree at least 8 m from, and slightly above, an active nest using a modified mobile antenna mount. Rotation of the mount in 2 planes allowed aiming the camera at a nest without repositioning the entire mount.

Although our time interval between exposures ($\bar{x} = 1.48$ min) probably missed some brief nest visits by adults, those behavioral sequences discussed herein were adequately sampled. Visits by food-carrying adults during late nestling stages were probably too short to be consistently recorded, but were evidenced by subsequent periods of nestling self-feeding, observable on the photorecord.

We installed cameras when oldest nestlings were 3, 10, 13, and 21 days old, at the 4 monitored nests respectively, and continued filming until nestlings fledged (i.e. left the nest during the day). Ages of nestlings during filming, number of frames exposed, and total duration of photorecording is tabulated for each nest (Table 1). Film and camera-advance batteries had to be changed every 6 days. All gaps in coverage were caused by the failure of a mechanical trigger to activate single-frame film advance in the cameras.

We analyzed time-lapse exposures by passing the processed film through an adapter in a 5 × 5 cm slide projector and viewing the enlarged image on a screen. The behavior depicted in each frame was categorized and behavior sequences were timed from the known exposure interval. Behavior categories included: adult brooding, adult feeding young, adult present (neither feeding nor brooding young), young feeding themselves, young standing (at least 2 of 3 nestlings standing in the nest), and young reclined. We later calculated the mean percentage (data from 4 nests combined) of time spent in each activity for each day of the nestling period, for determinations of behavioral trends.

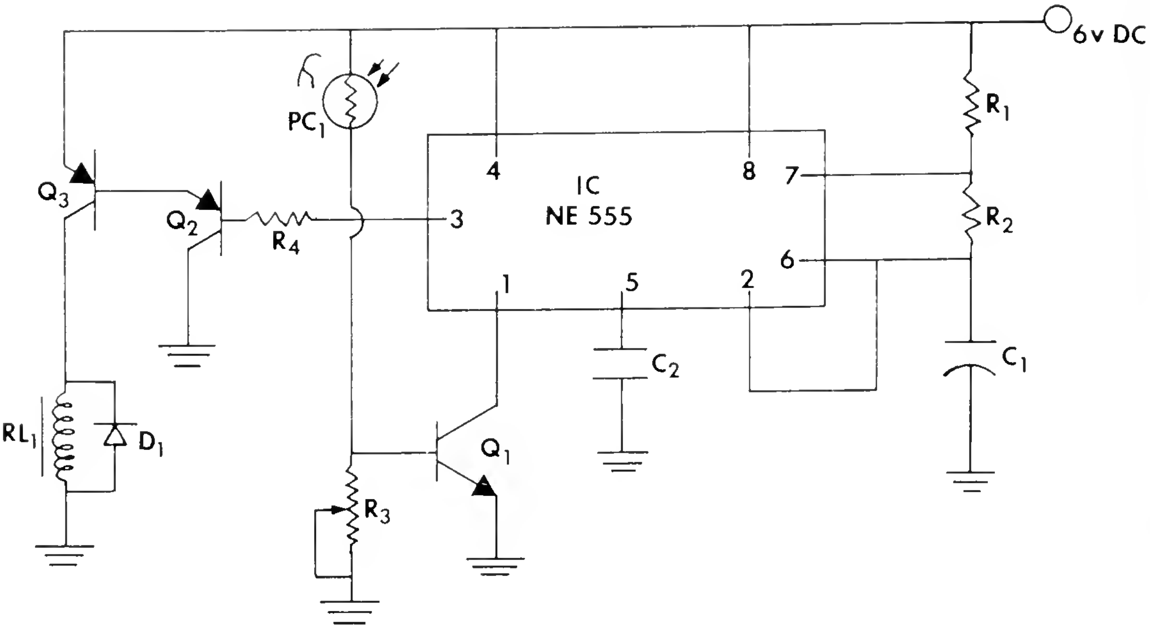

FIG. 1. Light controlled intervalometer circuitry for time-lapse photorecorders used to record activity at Red-shouldered Hawk nests. Components: R_1 = 15K–750K (timing resistor), R_2 = 10K, R_3 = 10K Pot, R_4 = 800 ohm, C_1 = 75uf–300uf (timing capacitor), C_2 = .01uf, Q_1 = 2N1308 or equiv, Q_2 = 2N3250 or equiv (select for HFE 40 min, R_4 = 800 ohm, I_{B2} = 7.5mA will give I_BQ_3 300mA), Q_3 = 2N4387 or equiv, PC_1 = CL904 or equiv, RL_1 = relay 6V3A, D_1 = 1A 30V PIV, IC_1 = 555 timer.

RESULTS AND DISCUSSION

Nesting chronology and survival.—Red-shouldered Hawks first appeared in the study area during the first week of March. Most adults were paired, territorial, and vociferous at this time. Courtship flights continued from 7 to 25 March and most commonly occurred between 11:00 and 13:00 on clear days. During the last week of March and first week of April, adults repaired and decorated old nests by the addition of dead twigs and fresh evergreen (usually hemlock) sprigs. Egg-laying was usually completed by mid-April; we noted incomplete clutches from 4 to 18 April 1974. Clutch-size ranged from 2 to 4 and averaged 3.33 eggs per nest (N = 9). Hatching occurred from 8 to 24 May 1974: at 3 nests where hatching rate was determined, 8 of 11 eggs hatched. Most fledglings left the nest between 25 June and 5 July. Ten of 14 hatchlings in 5 monitored nests successfully fledged; mortality at these nests was caused by Great-horned Owl predation (the entire 28-day-old brood at 1 nest) and by wind and possible hail (one 20-day-old nestling found dead under its nest after a thunderstorm).

Nesting habitat.—All of approximately 110 separate Red-shouldered Hawk sightings during 1974 occurred within the central strip of riparian habitat

TABLE 1

PHOTORECORDER FILM COVERAGE AT 4 RED-SHOULDERED HAWK NESTS IN MASSACHUSETTS, 1974

Nest no.	Extent of nestling period (days)	Time interval(s) (min)	Inclusive ages of nestlings during filming[a]	No. of days covered	No. of frames exposed	Total film-hours
1	28[b]	1.5	3–5	3	1,488	37.2
2	40	1.4	10–13, 16–26, 29–40	27	12,061	281.4
3	32	1.2	13–18, 25–32	14	6,846	136.9
4	39	2.1	21–26	6	2,016	70.5
		1.2[c]	29–31, 33–39	10	4,113	82.3
	TOTAL				26,524	608.3

[a] Nestling age is based on age of the oldest chick in each nest. Gaps in film coverage were due to camera failures.

[b] Brood killed by Great-horned Owl on day 28.

[c] Time interval was changed at day 29 post-hatch.

on Prescott Peninsula. Twenty-five percent of these sightings represented hawk hunting excursions which we watched from lookouts above the canopy. Six courtship flights in March 1974 likewise took place over wetlands and proximate slopes. This attraction for wet lowland habitat has been well documented (Kennard 1894, Henny et al. 1973, Wiley 1975).

All 12 nest sites found during our 2-year study were located in wet deciduous woods, as evidenced by the dominance of wetland tree species in sample plots around the nest tree: 32% black and yellow birches, 25% red maple, 16% sugar maple, 12% red and black oaks, 7% white ash, 6% white pine, and 2% assorted uncommon species. Tree density and mean DBH were fairly constant at the 12 nest-sites (Table 2) and indicated a mature forest stand. Nest tree DBH and height also varied little as nests were commonly placed in the largest deciduous tree available within a breeding pair's nesting habitat.

Black and yellow birches, comprising only 32% of all mature trees within sample plots, were chosen as nest sites 67% of the time. Stewart (1949) and Henny et al. (1973) also found most Red-shouldered Hawks' nests in black birch in Maryland. This preference for birch was probably related to its physical structure. Mature black and yellow birch trees supported few branches below 10 to 14 m; at this height many large branches extended laterally to form a platform, whereon nest construction and maintenance probably required less energy. Also, consistent nest height (Table 2) was probably related to this uniform branch divergence at 10 to 14 m.

TABLE 2

TOPOGRAPHICAL AND VEGETATIVE FEATURES OF RED-SHOULDERED HAWK NEST-SITES IN CENTRAL MASSACHUSETTS

		Nest site vegetation[a]		Nest tree			
Nest no.	Slope aspect	Forest density (trees/ha)	Mean tree DBH (cm)	Species	DBH (cm)	Height (m)	Nest height (m)
1	N,NE	778.1	18.0	*Betula nigra*	57.6	19.0	12.4
2	E,NE	622.5	22.6	*Betula nigra*	37.6	19.4	14.0
3	E	551.7	19.2	*Betula nigra*	51.4	26.0	13.4
4	E	636.6	22.7	*Betula nigra*	43.6	28.0	14.6
5	E	550.4	23.9	*Betula nigra*	57.9	18.2	11.5
6	NE	580.0	25.1	*Betula nigra*	61.8	20.6	12.9
7	E	565.9	16.1	*Quercus velutina*	53.5	28.0	9.8
8	E	693.2	21.0	*B. papyrifera*[b]	39.5	23.6	12.8
9	NE	707.3	21.8	*Acer rubrum*	30.2	29.6	10.6
10	NE	382.0	23.4	*B. lutea*	50.9	38.4	10.6
11	E	677.4	18.3	*B. lutea*	55.7	25.2	9.0
12	NE	551.7	21.8	*Acer saccharum*	41.1	24.8	11.8
$\bar{x}$		608.1	21.2		48.8	25.1	12.0
SD		102.1	2.3		7.3	5.5	1.7

[a] Trees of at least 5 cm DBH within 15 m of nest tree.
[b] American white birch.

Distances between adjacent active nests found on Prescott Peninsula in 1974 ranged from 0.9 to 3.0 km and averaged 1.7 km (N = 7), with nests arranged almost linearly along the central strip of streams and beaver flowages.

The adaptive value of nesting on strictly east or northeast slopes (Table 2) is difficult to explain. (Although we did not sample topography and vegetation on other slopes, it appeared that similar nest sites [i.e. mature black birch] and nesting habitat [i.e. wet woodland] were available on south and west slopes.) We could find no mention in the literature of slope aspect preferences by other nesting raptors. Perhaps the habit is practically neutral in adaptive value and has become traditional within this specific population, being learned by nestlings who as adults were attracted to nest sites most like their natal nest.

Nestling food.—Errington (1932) listed various problems encountered in accurately enumerating the prey individuals represented in nestling buteo pellets. Additionally, we observed that most mammalian prey were already decapitated when delivered to nestlings: therefore, jaw fragments and teeth, which might otherwise have survived gastric digestion, were usually excluded from nestling diets. Besides making prey identification more difficult, the absence of these remains in pellets made actual counting of individual food items impossible. We therefore recorded the occurrence of all prey species in each discrete pellet and calculated percent frequency for each species based upon the 212 pellet total (Table 3).

As reported elsewhere (New York, Ernst 1945; Maryland, Stewart 1949; Michigan, Craighead and Craighead 1956: and California, Wiley 1975), Massachusetts red-shoulders preyed most often upon small mammals, specifically eastern chipmunks (*Tamias striatus*). The frequency of hawk predation on chipmunks was apparently related to this sciurid's abundance in the springs of 1973 and 1974. Also, reproduction in Massachusetts hawks coincided with the availability of their principal prey—hatching coincided with emergence from burrows of young-of-the-year chipmunks (D. Snyder, pers. comm.).

During our observations from blinds, we observed the delivery of 46 prey items to nestlings; species representation paralleled the results of pellet analyses (Table 3) except for a much higher incidence of frogs (*Rana* spp.), which were probably completely digested and excluded from pellets. Similarly, Snyder and Wiley (1976) observed (from blinds) that 50 reptiles and amphibians were delivered to a Florida Red-shouldered Hawk nest during the same period that only 8 reptile and amphibian prey were counted in pellets.

Sex roles.—Sexual dimorphism in adult red-shoulders was not apparent: we were therefore unable to treat male and female adult behaviors separately. Only 1 adult was visible at the nest on all but 3 of over 26,000 photorecorder exposures, suggesting to us a distinct separation of sex roles in rearing the brood. If both adults shared nest duties, we believe the photorecord would have shown many more interactions involving both adults at the nest, especially during early nestling stages when adult attentiveness was most intense (see below).

Often while observing nests from blinds, we saw the departure of an attentive adult immediately after we had heard the nearby call of (presumably) its mate. Within 30 sec to about 5 min after such an interchange, an adult returned to the young carrying food. On 5 occasions at 2 different nests, the adult that originally left the nest was so marked, by a peculiar bloodstain on the cere, that it could be distinguished from its mate: on these occasions the same adult that departed the nest also returned with food and remained the only attentive adult throughout the day of observation. These few observations invite the hypothesis that 1 member of the pair (tentatively the hunting male) delivers prey to the nest vicinity and transfers the food to his mate (the female) who attends and feeds the nestlings.

TABLE 3

RED-SHOULDERED HAWK NESTLING DIET DETERMINED BY PELLET ANALYSES AND BY VISUAL OBSERVATIONS FROM BLINDS, CENTRAL MASSACHUSETTS, 1974

	Pellet analyses		Visual observations	
Species represented	No. of pellets containing remains	Percent[a]	No. of occurrences	Percent[b]
Mammalia	211	99.5	33	71.7
Tamias striatus	138	65.1	20	43.5
Peromyscus leucopus[c]	20	9.4	2	4.3
Parascalops breweri[d]	19	9.0	2	4.3
Blarina brevicauda[e]	16	7.5	4	8.7
Sorex cinereus[f]	6	2.8	0	0
Microtus pennsylvanicus[g]	5	2.3	0	0
Clethrionomys gapperi[h]	5	2.3	0	0
Tamiasciurus hudsonicus[i]	2	1.0	0	0
Unidentified	0	0	5	10.9
Aves	7	3.3	2	4.3
Unidentified	4	1.9	0	0
Cyanocitta cristata[j]	3	1.4	2	4.3
Reptilia	49	23.1	2	4.4
Colubridae[k]	48	22.6	0	0
Thamnophis sirtalis[l]	1	.5	1	2.2
Opheodrys vernalis[m]	0	0	1	2.2
Amphibia	1	.5	9	19.6
Rana spp.[n]	1	.5	9	19.6
Insecta	2	1.0	0	0
Coleoptera[o]	2	1.0	0	0

[a] Based on analyses of 212 discrete pellets collected at 7 nests.

[b] Based on 46 food items delivered to 4 nests.

Common names not included in text: [c] white-footed mouse, [d] hairytail mole, [e] shorttail shrew, [f] masked shrew, [g] meadow vole, [h] boreal red-backed vole, [i] red squirrel, [j] Blue Jay, [k] unidentified colubrid snakes, [l] eastern garter snake, [m] smooth green snake, [n] unidentified frogs, [o] unidentified beetles.

Matray's (1974) study of sex roles in the Broad-winged Hawk, a congener of the red-shouldered, lends credence to this hypothesis.

Obviously, the role of the sexes in Red-shouldered Hawk nesting needs to be studied further, ideally by individually marking each member of a pair, and especially if the sex of marked adults can be determined in the field.

Feeding interactions—visual observations.—The approach of an adult hawk to the nest was always heralded by a chirping call emitted by nestlings. This call was continued after the adult's arrival whether or not food was

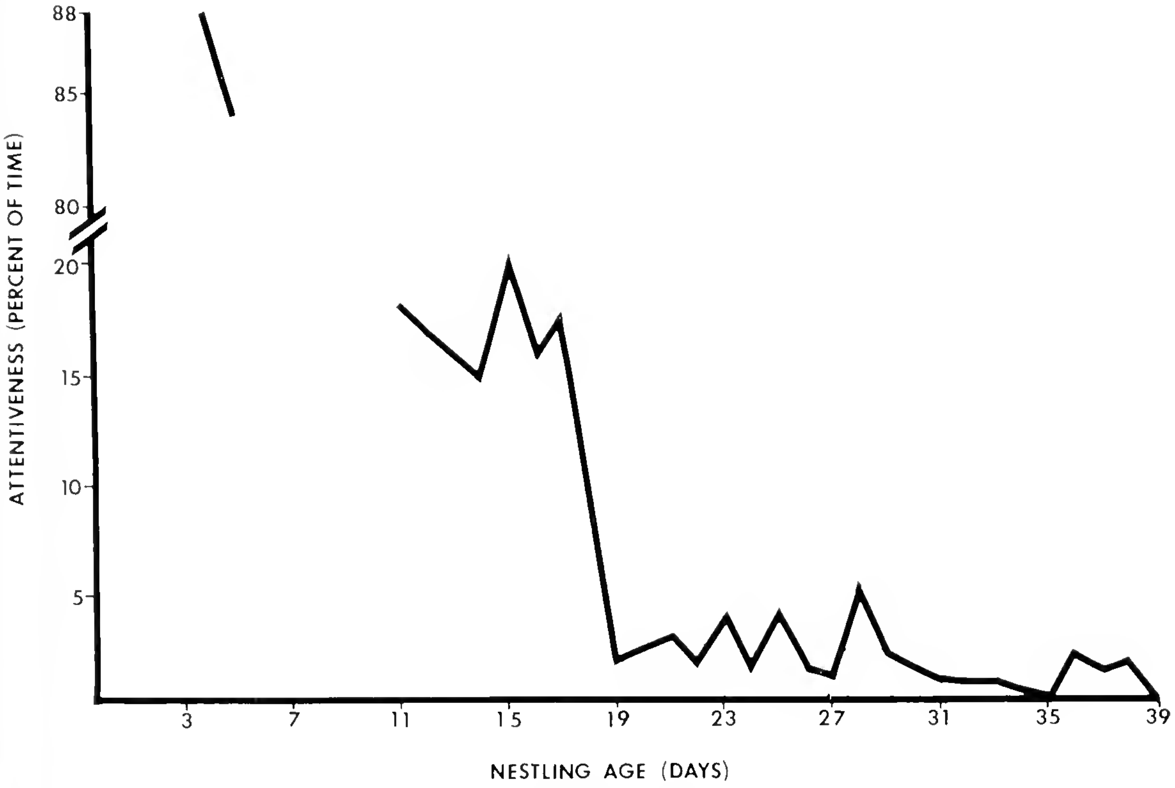

Fig. 2. Changes in adult Red-shouldered Hawk nest attentiveness with advancing nestling age.

delivered. Nestlings, even when large and fully feathered, never attempted to snatch or feed upon prey held by a parent but chirped intermittently until the adult either began feeding them or departed.

When being fed, nestlings gathered side by side before a parent bird. Meanwhile, the adult stood upon the carcass and with its beak tore away strips of flesh. When each piece of meat was presented before the nestlings the closest or most aggressive bird moved toward the proffered food. The adult immediately responded, slowly and deliberately placing the food in the nestling's open beak. Although adults initiated each feeding episode, it was apparently the movement of nestlings towards presented food that triggered the response of relinquishment in adults.

Young became capable of some self-feeding by day 18: however, throughout the nestling period an adult that arrived at the nest and encountered nestlings ineffectually pulling at prey always seized the carcass, tore off pieces of flesh, and offered these to the young. This adult reaction to incompetent nestling feeding appeared similar to the adults' response to movement toward food by downy young.

As the nestlings matured and became more adept at tearing food and thereby feeding themselves, they rarely fed upon a prey item simultaneously.

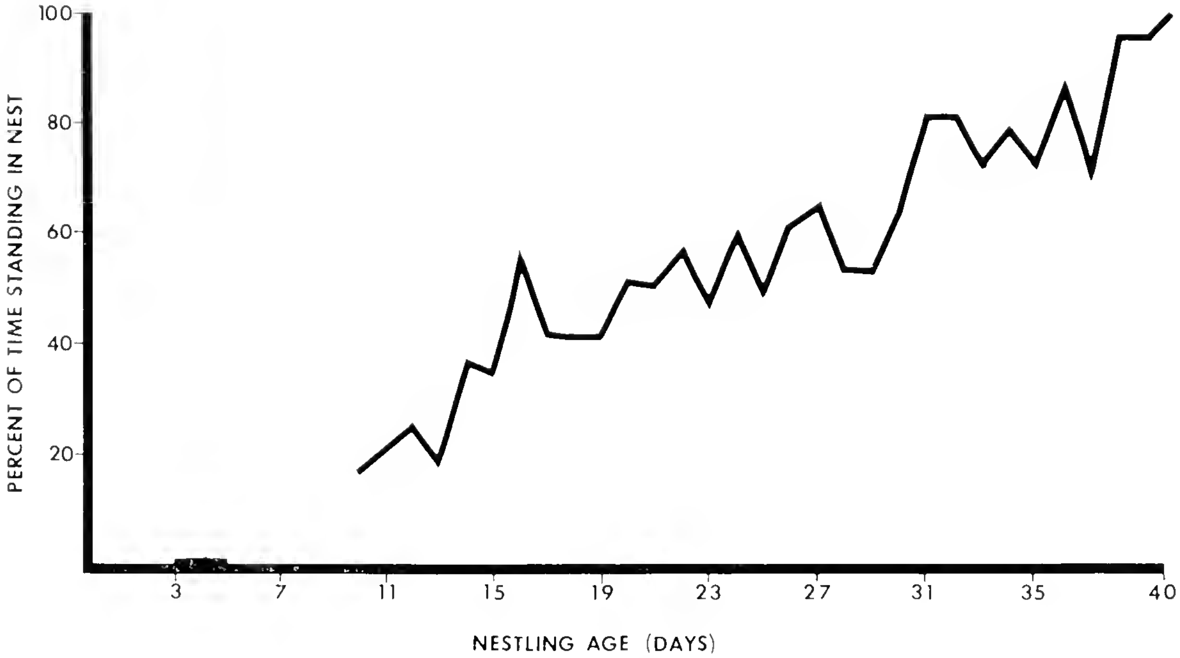

FIG. 3. Changes in nestling Red-shouldered Hawk activity with advancing age.

especially when active and hungry after a fast of several hours. Instead, a prey animal delivered to the nest by an adult would be seized by a single nestling. Other nestlings would then emit the above-mentioned chirping call with head directed and neck extended toward the feeding nestmate. This "pleading" behavior was immediately followed by a "hoarding" posture on the part of the nestling who held the food, i.e. the feeding bird stood over the carcass with lowered wings, tail, and head, and usually continued feeding. Chicks never tried to grasp food from their nestmate when the latter maintained this hoarding posture. However, when pleading failed to stimulate a hoarding response, prey was quickly snatched by a sibling who likewise displayed the hoarding behavior when a pleading nestmate approached. Hoarding was performed only by nestlings possessing food and only while nestmates pleaded. Agonistic encounters were never observed among nestmates and evidently the "pleading–hoarding" behavior pattern had adaptive value in effectively reducing violent strife.

Nestlings exhibited gular flutter when the nest was exposed to direct sunlight and ambient temperatures exceeded 26° C. Sudden gusts of wind were usually followed by vigorous wing-flapping in chicks 20 days old or older.

Nineteen times throughout the nestling period, at 3 different nests, we recorded the arrival of an adult carrying a green deciduous, hemlock, or pine (*Pinus* spp.) sprig in the beak. The adult carefully arranged this

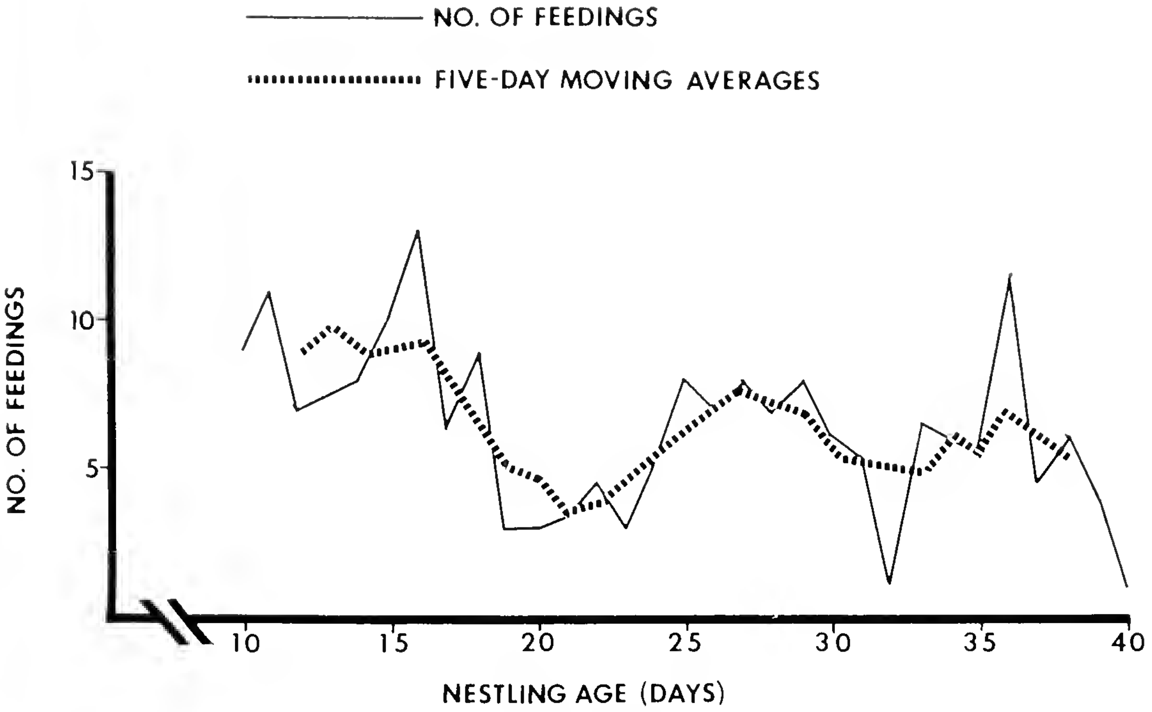

FIG. 4. Changes in mean number of daily feedings as nestling Red-shouldered Hawks grow.

material on the nest before departure. This behavior appeared to increase in frequency as nestlings grew.

Photorecord and behavior quantifications.—A total of 26,524 time-lapse exposures representing 608.3 film hours was obtained from photorecorders at 4 active nests (Table 1). All 4 nests contained 3 nestlings during filming so that energy demands, and therefore feeding rates, were comparable and data were combined in graphing behavioral trends.

Adult attentiveness, mainly brooding, was the dominant behavior at the nest during the first week following hatch (Fig. 2). Nestling activity steadily increased. From day 19 until fledging, attentiveness rarely exceeded 10 min per day and consisted almost entirely of brief feeding sequences: meanwhile nestling activity continued to increase linearly (Fig. 3).

Mean number of feedings per day has been calculated and trends clarified by computing 5-day moving averages (Fig. 4). The decrease in feedings per day from day 16 to 21 represented the reduction in adult feedings as nestlings began feeding themselves from prey remains left in the nest. From days 22 through 27, rapidly growing young required more energy: therefore, a greater number of prey items were delivered by adults, accounting for the increase in recorded feeding sequences. This increase in energy demand is also reflected in the total time spent feeding per day (Fig. 5) after day 22.

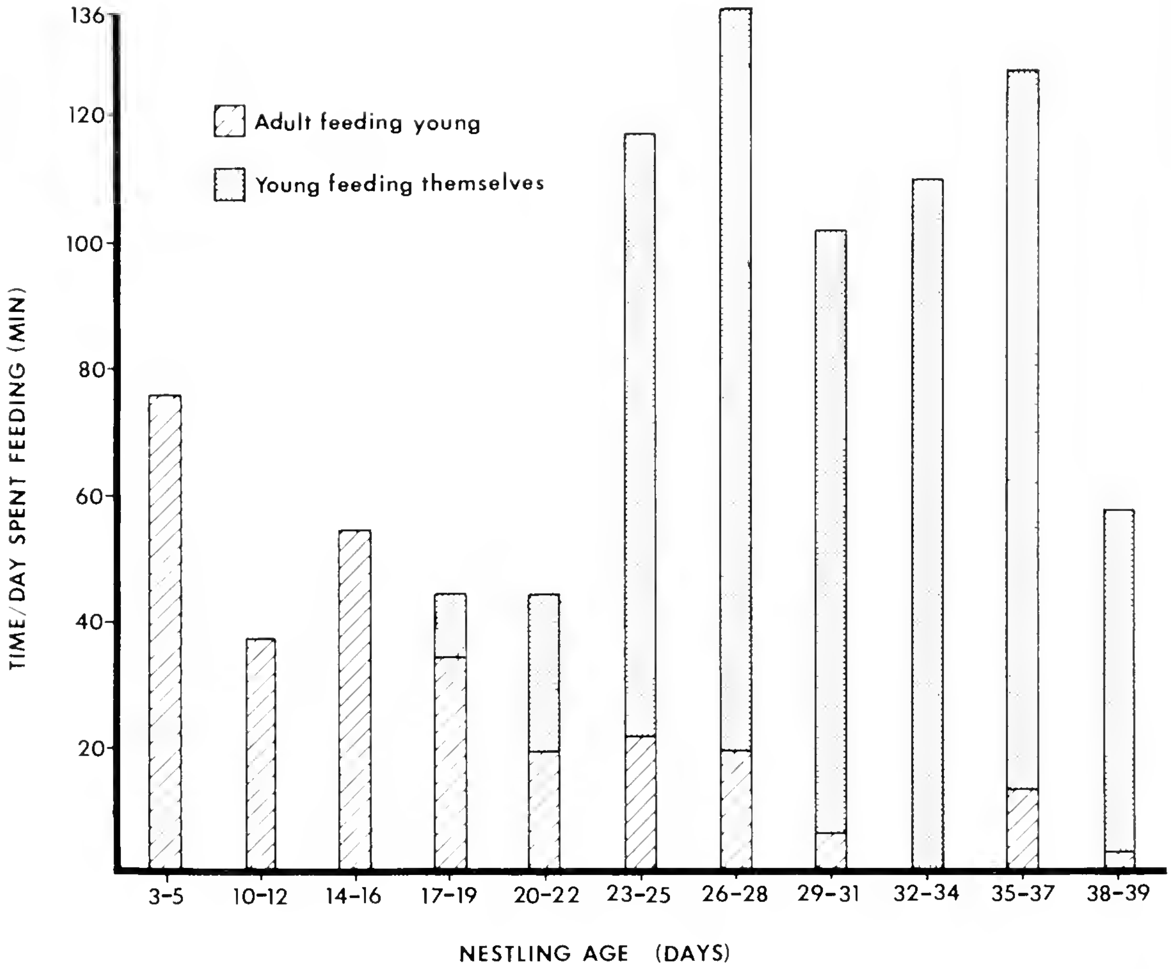

FIG. 5. Changes in the total time spent feeding per day by nestling Red-shouldered Hawks.

We computed the mean duration of adult and nestling feeding sequences for each day of photorecord from four 1974 nests (Fig. 6). Adult feedings took longest during the first few days following hatching, when prostrate nestlings required most assistance.

After the first few days of the nestling period, we observed a gradual reduction in duration of adult feedings, but no important changes in duration of self-feeding sequences by nestlings after day 18 (Fig. 6). An 8.1 min overall difference in mean feeding duration between the 2 types of feeding sequences was in part due to the difference in feeding proficiency between adults and young. Increased food intake also contributed to the time spent feeding by nestlings over 21 days old.

Feedings occurred more frequently between 08:00 and 16:00 than either between 06:00 and 08:00 or between 16:00 and 20:00 (ANOVA, $P < 0.05$). The gradual increase in the number of feedings from dawn through late

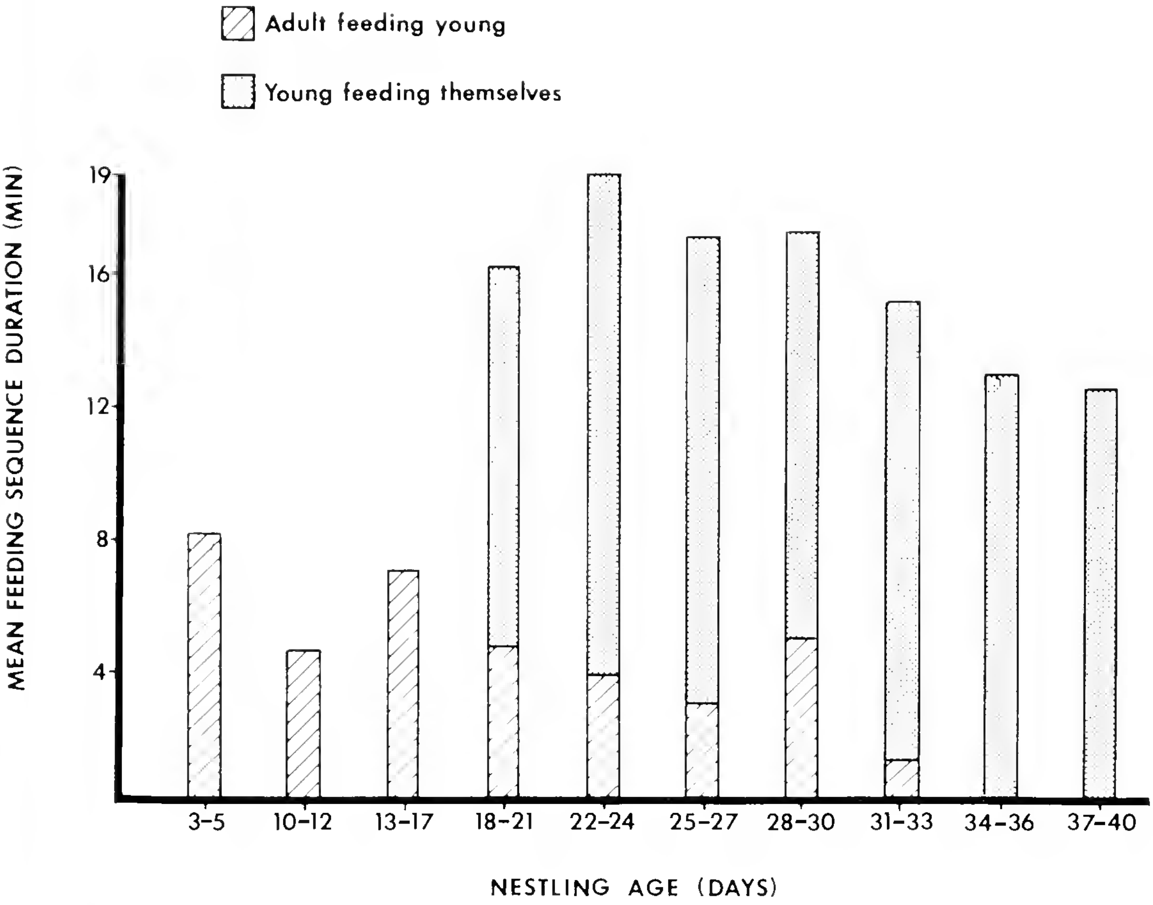

FIG. 6. Comparison of mean feeding sequence duration with respect to adult Red-shouldered Hawk feedings and nestling self-feedings throughout the nestling period.

morning reached a peak between 14:00 and 16:00, and gradually decreased from 16:00 until dark (Fig. 7). It would be interesting to compare this diurnal dispersion of feeding sequences, and presumably successful prey captures, with the activity patterns of principal prey species. Unfortunately, the activity patterns of chipmunks have not to our knowledge been documented.

SUMMARY

A study of Red-shouldered Hawk (*Buteo lineatus*) nesting ecology and behavior was conducted during 1973–74 in a 5000 ha reservoir watershed in central Massachusetts. Courtship occurred in March, egg-laying and incubation in April, hatching in mid-May, and fledging in late June and early July. Mean clutch-size was 3.33 (at 9 nests), hatching rate was 73% (at 3 nests), and 71% of hatchlings fledged (at 5 nests). Hawks hunted and nested along the central strip of riparian habitat on the peninsular study area. Inter-nest distances averaged 1.7 km ($N = 7$, range: 0.9–3.0 km) in 1974. All nests ($N = 12$) were situated in mature deciduous trees, usually black birch (*Betula nigra*), on east or northeast slopes. Eastern chipmunks (*Tamias striatus*) were the

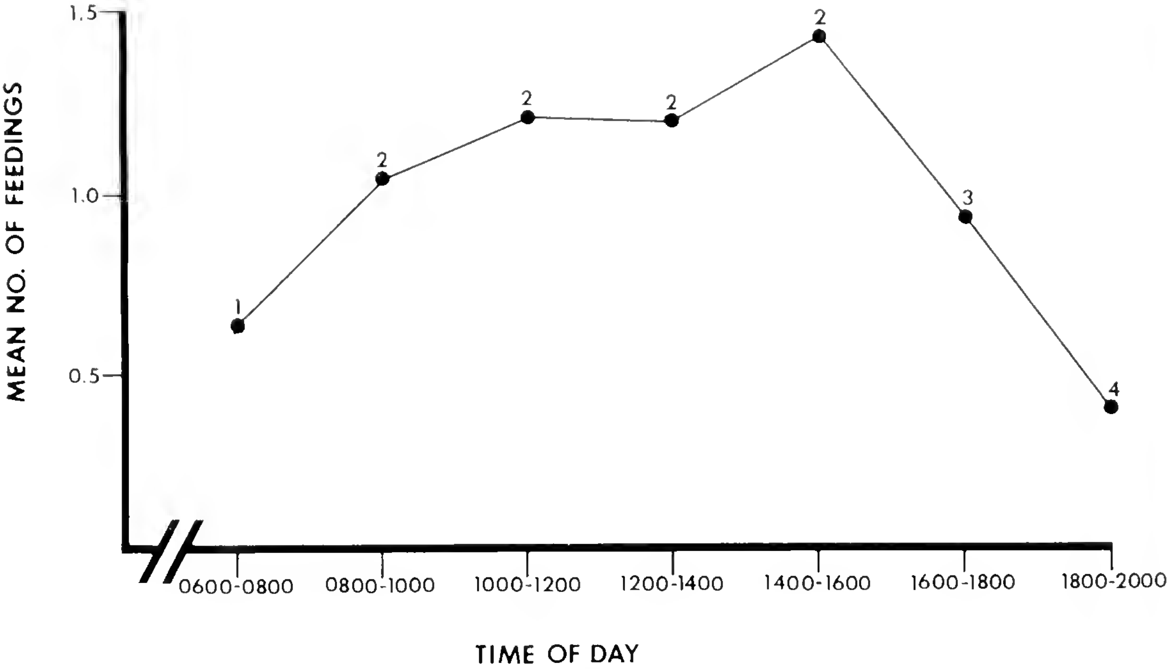

FIG. 7. Diurnal dispersion of feeding sequences (i.e. prey deliveries) at 4 Red-shouldered Hawk nests over 30 nesting days. Adjacent data points having dissimiliar superscripts are significantly different ($P < 0.05$) from each other.

principal prey fed to nestlings. Interactions of nestlings and adults during feeding are described. Behavioral trends throughout the nestling period were quantified at 4 nests using time-lapse automatic cameras. Adult attentiveness decreased rapidly from day 4 to day 19 post-hatch. Nesting activity increased linearly from day 10 to fledging. The number of feeding sequences per day decreased from day 10 to day 19, increased from day 20 to day 25, and then remained stable until the decrease just before young left the nest. Nestling self-feeding sequences averaged 8.1 min longer than adult feeding sequences. Feedings occurred more frequently between 08:00 and 16:00 than during early morning or late afternoon.

ACKNOWLEDGMENTS

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Wilson Bull., 91(1), 1979, pp. 118–122

GENERAL NOTES

Nest selection by Brown-headed Cowbirds.—Brown-headed Cowbirds (*Molothrus ater*) are brood parasites: their eggs are laid in the nests of other species. Norman and Robertson (Auk 92:610–611, 1975) describe behavior by which cowbirds have been observed to find nests. Activity of potential hosts about nests—when building, laying eggs, and incubating—can serve to attract some attention to the nest and to identify nesting stages to cowbirds. Additionally, female cowbirds may be successful in searching for nests without seeing host activity, though such potential has not been well documented.

Thompson and Gottfried (Wilson Bull. 88:673–675, 1976) experimentally tested the prerequisite of host activity at the nest for cowbird parasitism by setting out nests with 2 Japanese Quail (*Coturnix coturnix*) eggs followed by daily examination of nests for changes in contents. They made a total of 240 of these nestings over 12 weeks, and observed no cowbird activity. I similarly tested for the requirement of host activity and also examined variation in habitat, nests, and eggs in terms of possible cowbird preferences.

Methods and materials.—Egg shells were filled with agar and the hole sealed with paraffin. Length and width of these eggs were measured as well as spot size and density. Fig. 1 shows variation in appearance of eggs used in 1977. During 1978 egg shells of Barn Swallows (*Hirundo rustica*) were used for the most part. "Clutches" were composed of eggs similar in size and appearance. In some cases intact House Sparrow (*Passer domesticus*) eggs were used to compose clutches. These eggs were placed in nests, 1 per day, to produce clutches of 2, 3, or 4 eggs. Nests were checked daily thereafter for a total of 10 days. Damage to or disappearance of eggs was noted. This procedure similated the egg-laying and initial incubation period of birds.

Experimental nests were nests that had been used the previous year or earlier in the season, and were no longer active. The nests, showing varying degrees of weathering, were of open cup construction and included nests of the following species: American Robin (*Turdus migratorius*, 2 nests), Bell's Vireo (*Vireo bellii*, 1), Northern Oriole (*Icterus galbula*, 1), Red-winged Blackbird (*Agelaius phoenicus*, 4), Cardinal (*Cardinalis cardinalis*, 3), American Goldfinch (*Carduelis tristis*, 3), Field Sparrow (*Spizella pusilla*, 6), and 5 unidentified nests. Some were retained in the position where they were built; others were inserted into woody vegetation. Heights of these nests ranged from 0.4 to 2.6 m above ground.

Three series of experimental "egg-laying" were conducted. The 2 series in 1977 included 10 nests each: 1 began on 10 May 1977 and the other on 2 June 1977. The last series started 16 May 1978 and involved 13 nests. All nests were within a 9 ha area of second growth on the West Campus of the University of Kansas, in Douglas Co., Kansas.

Based on the mean values for each clutch, eggs could be described by 2 dimensions of variability determined by egg size and marking pattern. Egg size is approximate egg volume given by $V = 0.512\ LB^2$, where L is egg length and B is egg width (Stonehouse, Emu 65:227–228, 1966). Egg marking pattern was measured on a subjective scale, determined in part by spot size and density, that ordered eggs from light to dark in appearance. In addition to locating the experimental clutches on these axes, I did the same for 50 Kansas open-nesting passerine species. The species were selected from Zimmerman's (Kansas Ornithol. Soc. Bull. 20:13–16, 1969) report on the 1968 Breeding Bird Survey for Kansas. The suitability of these species as cowbird hosts was determined from information in several sources (Friedmann, U.S. Natl. Mus. Bull. 233, 1963; Auk

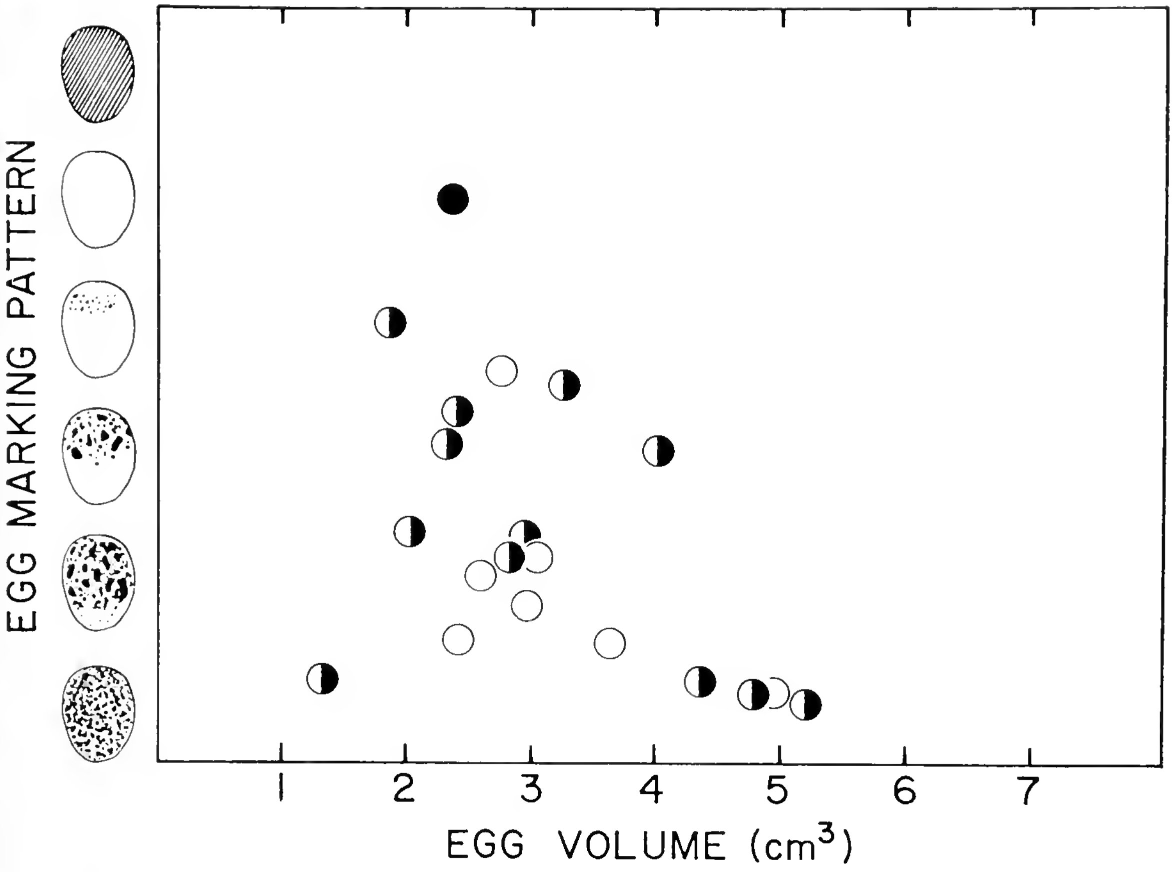

Fig. 1. The experimental clutches of 1977 located on axes of marking pattern (darkness) and size (volume). Solid circle—parasitized clutch; half-solid circle—clutches from which single eggs disappeared; open circles—others. Egg pattern examples are (from top): Gray Catbird (*Dumetella carolinensis*) (a blue egg); Eastern Phoebe (*Sayornis phoebe*); vireos; Yellow-breasted Chat (*Icteria virens*), or Orchard Oriole (*Icterus spurius*); Cardinal or House Sparrow; Brown Thrasher (*Toxostoma rufum*). The parasitized clutch in 1978 was lightly spotted and 1.9 cm^3.

88:239–255, 1971; Friedmann et al., Smithson. Contrib. Zool. 235, 1977; Elliott, Auk 95:161–167, 1978; Hill, Wilson Bull. 88:555–565, 1976; Rothstein, Condor 77:250–271, 1975). I used illustrations in Reed (North American Birds Eggs, Doubleday, Page & Co., New York, 1904) for egg marking patterns and Bent's Life History series (U.S. Natl. Mus. Bull. 179, 191, 195, 196, 197, 203, 211, 1942–1968) for egg sizes. The variation in egg appearance of Kansas passerine birds is illustrated in Fig. 2, as is the relative abundance of each species and their suitability for cowbirds, and shows the egg universe to which Kansas cowbirds are exposed.

Nest size and construction is not dealt with here except for incidental comments. In general I placed larger eggs into nests with larger inside diameters. I tried to measure nest exposure but found no easy way to do this. Nests were not completely concealed from view when I was within a few meters of them.

Results.—Two instances of cowbird parasitism were noted—1 each year. One occurred in an American Goldfinch nest (built the previous year and still in its original site) situated at the edge of a thicket of sapling elms (*Ulmus rubra*) and placed 226 cm above

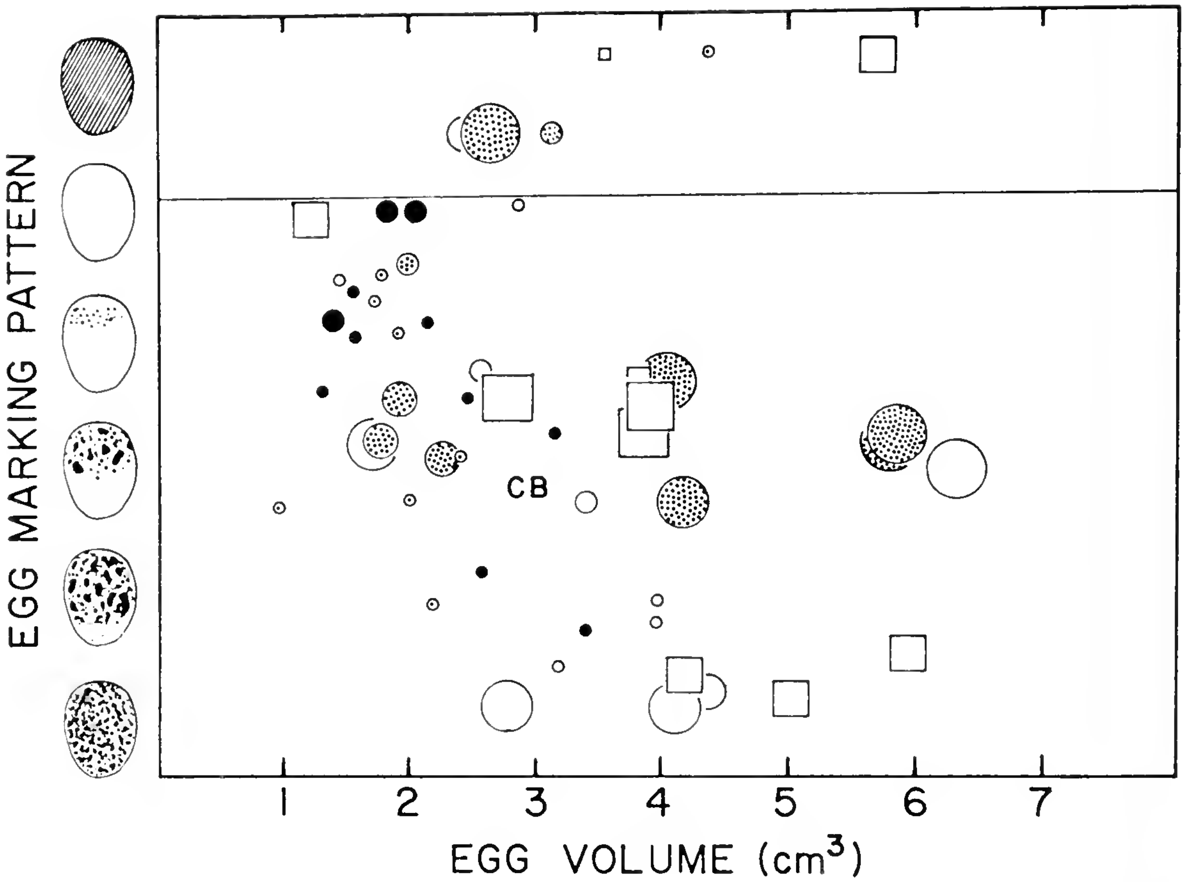

FIG. 2. Egg variation of Kansas open-nesting passerines ordered on the same scale as Fig. 1. Symbol size shows relative abundance of each species (see Zimmerman, 1969): smallest to largest symbols—less than 1 bird per census route, 1.0 to 4.9, 5.0 to 9.9, 10.0 to 29.9, 30.0 to 75.0. Solid circles—abundantly parasitized, good host species; stippled circles—moderately parasitized, good hosts; open circles—incidental hosts; squares—rejector species and poor hosts. CB shows position of cowbird eggs.

the ground. The clutch assigned to this nest was of phoebe-like eggs. The first of 4 eggs was placed in the nest on 10 May 1977. This egg was missing the following day when the second was added. The third egg (making 2 in the nest) was inserted the next day. When I added the last egg on day 4, the second egg was missing. On 14 May, nest contents were the fourth egg and a cowbird egg. On 15 May only the cowbird egg, with a hole in the side, remained in the nest. This egg was then removed by me. The other instance occurred in an old Northern Oriole's nest inserted 190 cm above ground in an elm sapling. Barn Swallow eggs were "laid" in this nest on 17 and 18 May 1978. On 22 May the contents were 1 "host" egg and 1 cowbird egg. The nest was empty the next day.

Several instances were observed when only 1 egg from the clutch disappeared, suggestive of cowbird activity, i.e. removal of a host egg prior to cowbird laying (Friedmann, op. cit.). During 159 nest-days of observation at the 20 experimental nests in 1977, the disappearance of 1 egg, as sole nest contents, happened 11 times and, as part of a clutch, 11 times. There were 15 other instances of loss or damage to contents of experimental nests; only 2 of the 20 nests were completely free from losses. I once saw a black rat snake (*Elaphe obsoleta*) at an experimental nest with eggs missing. Damaged eggs appeared frequently to have been pecked; once a missing egg was found about 20 m away from its nest with a puncture in the side. Thus, snakes and birds were likely predators of some eggs.

During the experiments there were 3 times that I prepared a mixed clutch: 2 eggs of similar size but different in pattern—1 (a House Sparrow's) cowbird-like and the other much less spotted. Twice, 1 egg disappeared leaving the more cowbird-like egg.

Cowbird activity was shown twice by the appearance of a cowbird egg; host activity about the nest is not an absolute requirement for cowbird parasitism. Additional cowbird activity was suggested by predation of single eggs, especially by the disappearance of an egg not cowbird-like from mixed egg clutches.

Discussion.—Brown-headed Cowbirds can find nests by searching and need not observe activity of host birds at the nest. The cowbird eggs elicited by these experiments were laid at an "appropriate" time—at the start of or early in incubation. These observations and others at nests from which single eggs disappeared hint of exploratory visits to nests. Perhaps further parasitism was stopped as other nests were discovered not to have real eggs. The overall parasitism rate in my experiment, 6% of the nestings presented, however, is lower than parasitism rates of Kansas bird populations studied by Hill (1976). Of 1218 passerine nests observed by Hill (including 712 of host species), 166, or 14%, were parasitized. The mere presence of nests and eggs does not result in a "normal" parasitism rate. Thus the importance of host activity as aids for cowbirds to find nests cannot be discounted.

Thompson and Gottfried's (1976) experiment was not successful in inducing cowbird parasitism—possibly due to 2 features of their procedure. One—perhaps the more important criticism—is their use of *Coturnix* eggs. These eggs are large, generally much larger than usual host species ($V = 9.74$ cm^3; 1.6 times larger than meadowlark eggs and about 9 times larger than the smallest hosts' eggs). King (Am. Zool. 13:1259, 1973; pers. comm.) found egg size to be a very influential variable for inducing cowbird parasitism in captive birds—nests with larger egg sizes were avoided. The other feature of criticism is the use of 2 eggs placed in a nest together rather than simulating egg-laying. This criticism presupposes that cowbirds select nests preferentially during the egg-laying stage by responding to changes in nest contents. King (pers. comm.) found no evidence for such a preference in his experiments.

Most of the experimental nests were within the range of habitat preference of cowbirds determined by Lowther and Johnston (Kansas Ornithol. Soc. Bull. 28:36–40, 1977) for northeastern Kansas. Among 7 natural nests found in 1977, the only cowbird activity in the study area was at a Red-winged Blackbird nest. Three cowbird eggs were found in the nest on 26 April. (This nest was empty on 24 April after a visit by a black rat snake; the nest was again empty on 29 April. This nest was later used in the experiments.) In 1978, 3 parasitized nests were found during the course of the experiment. Two Red-winged Blackbird nests and 1 Cardinal nest were found with 7 cowbird eggs among them.

I saw, at most, 5 or 6 cowbirds on the study area. This number is indicative of cowbird density similar to that determined for a successional area censused by Cink and Paul (Am. Birds 29:1122–1123, 1975) only 3 km away. Experimentation was done during peak cowbird activity in Kansas (Lowther, Bird-Banding 48:358–369, 1977).

Egg variation for Kansas host species is shown in Fig. 2. Commonly used host species have eggs generally smaller and less marked than cowbird eggs. The eggs of the parasitized experimental clutches are decidedly within the size range of common hosts. Rejector species (Rothstein, 1975) and poor hosts have eggs differing from the size-marking range most often victimized by cowbirds. Brown-headed Cowbird eggs are themselves partly outside this range which may aid in preventing egg ejection by other female cowbirds (but see Elliott, Auk 94:590–594, 1977). Similarities of eggs of good and poor hosts are not always as close as suggested in Fig. 2. For example, Eastern Kingbird (*Tyrannus tyrannus*, a rejector) and Red-winged Blackbird (a fairly good host) eggs are similar in spotting density (my subjective opinion) and size, but are obviously different in background color and shape of markings. (This shows a real deficiency of my 2-dimensional representation of egg variation.)

Little attention was given to variation in nest structure. This deficiency, however, may not be critical. King (pers. comm.) found that nest variation is of minor importance in comparison to egg appearance, especially egg size. In my experiments, nest dimensions covaried with egg size across species: smaller eggs were in nests of smaller nest dimensions, larger eggs in larger nests. Any search image that cowbirds may use in selecting host nests could still include aspects of nest construction independent of egg appearance.

My interpretation can be questioned on several grounds. Most noteworthy is that neither were cowbirds observed nest searching nor were experimental nests watched for cowbird visits. Cowbirds are known to lay eggs in deserted nests, but events at these parasitized nests argue against non-deliberate egg-laying. Accurate knowledge of which nests were actually exposed to cowbirds would greatly aid in proper interpretation of my experiment.

Acknowledgments.—Stephen I. Rothstein, Robert B. Payne, Andrew P. King, Richard F. Johnston, Calvin L. Cink, and Karen S. Harris were most generous in their critical readings of the manuscript. Assistance on the design and operation of the experiment was provided by K. S. Harris, J. Gulbis, C. J. Terry, J. T. Paul, and C. T. Stahmann. M. A. Jenkinson allowed use of data-less eggs from the collections in the Museum of Natural History, University of Kansas.—PETER E. LOWTHER, *Museum of Natural History and Dept. of Systematics and Ecology, Univ. of Kansas, Lawrence, KS 66045.* *Accepted 31 Dec. 1977.*

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Cowbird parasitism on Common Bushtit nest.—While studying nest helping in Common Bushtits (*Psaltriparus minimus*) we observed an instance of Brown-headed Cowbird (*Molothrus ater*) parasitism on a bushtit nest. Previously, Bent (U.S. Natl. Mus. Bull. 191, 1946), Friedmann (U.S. Natl. Mus. Bull. 233, 1963; U.S. Natl. Mus. Bull. 149, 1966), and Friedmann et al. (Smithson. Contrib. Zool. 233, 1977) have reported a total of 8 cases of parasitism of this species in California and British Columbia. Among the reports from California were 1 cowbird egg in a nest with 8 eggs and 2 parasitized clutches that were partially buried under new nest linings. We believe clutch burying to be a sign of abandonment and not a part of normal incubation behavior.

The nest we observed was discovered on 30 April 1977, in a woodland portion of the University of Washington campus in Seattle. The nest was attached to a solitary arch of a blackberry vine (*Rubus* sp.) 1.5 m from the ground. On 1 May the female bushtit was captured in a mist net as she left the nest, and another bird, presumably her mate, was noted in the vicinity. The female was banded and weighed and no brood patch was evident. Her weight (7.7 g) indicated that she was laying. The nest contained 5 unincubated eggs. On 17 May the female was recaptured and weighed 6.3 g. This time she had a definite brood patch and continuously gave distress calls. The nest contained 6 warm eggs. A 20 min observation period on 18 May showed no activity at the nest, and we assumed that the female was incubating. On 24 May a tear was noted near the top of the nest. The nest contained 4 newly hatched, but dead nestlings, 2 unhatched eggs containing nearly fully developed embryos, and 1 cowbird egg showing no sign of development. We saw no adult birds in the vicinity and concluded that the nest had been abandoned. Freshness of the young suggested to us that the nest had been deserted within the past 2 days. It seems likely that the damage to the nest was caused by the cowbird when the egg was deposited, as has been reported for Verdins (*Auriparus flaviceps*) (Friedmann, op. cit., 1963) and for 1 of the cases of parasitism described from British Columbia (Friedmann et al., op. cit., 1977). Desertion may have occurred either in response to the damaged nest or to the presence of the cowbird egg.

Of 54 bushtit nests studied in 1977, this was the only case of cowbird parasitism. That the cowbird egg was deposited so late in the incubation period might off-hand suggest egg-dumping. However, since it was not late in the reproductive period of the species and since this event is not comparable to the well-documented dump-nests of Shining (*Molothrus bonariensis*), and Bronzed (*M. aenus*) cowbirds, it is perhaps better to regard it as a case of faulty timing by the parasite (Friedmann et al., op. cit., 1977). Since cowbirds lay clutches of eggs (Payne, Condor 78:337–342, 1976), a cowbird might resort to an inappropriate nest when not enough host nests are available.

We wish to acknowledge the help of Keith Bergman, Cynthia McCarthy, and Russ Ray with the field work and to thank Cynthia McCarthy, Donald S. Farner, Sievert A. Rohwer, and John C. Wingfield for their comments on this note.—Jan Peter Smith, *Dept. of Zoology, Univ. of Washington, Seattle, WA 98195, and* Riley J. Atkins, *206 N. 41st St., Seattle, WA 98103.* *Accepted 30 Nov. 1977.*

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Effect of food availability on leaf-scratching by the Rufous-sided Towhee: test of a model.—Many emberizine species scratch in leaves with a 2-footed kick to the rear under their bodies (e.g., Hailman, Wilson Bull. 85:348–359, 1973). The number of successive scratches given without a distinct pause (a "bout") was modeled quantitatively, and the model successfully predicted scratching behavior of White-throated Sparrows (*Zonotrichia albicollis*) and Dark-eyed Juncos (*Junco hyemalis*) (Hailman, Wilson Bull. 86:296–298, 1974). Later Hailman (Wilson Bull. 88:354–356, 1976) found that scratching of the White-crowned Sparrow (*Z. leucophrys*) and Fox Sparrow (*Passerella iliaca*) also conformed to prediction. These comparative data suggest that scratching obeys the same rules for all emberizines, although Hailman (1976:356) noted that "a check on the rather different towhees (*Pipilo*) would be desirable." We report our combined data for scratching by Rufous-sided Towhees (*P. erythrophthalmus*) in Tennessee, which include an experimental test by E.H.B. of the model.

The model states simply that the bird scratches until uncovering a potential food item, and that the probability of finding such an item is constant (independent of the number of scratches given previously in the bout). The model predicts that:

$$\log f_s = \log p(s-1) + \log B, \tag{1}$$

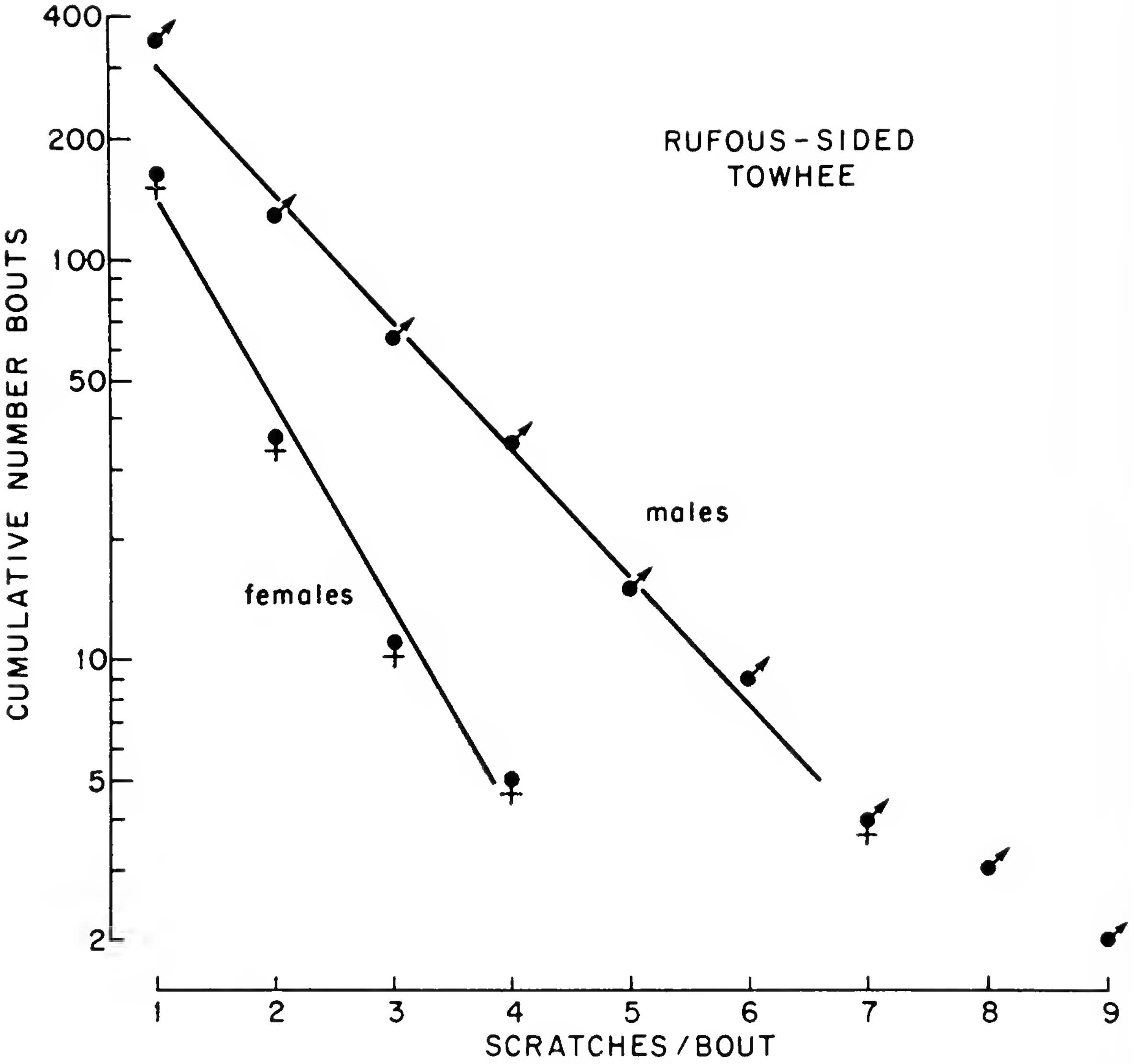

FIG. 1. Cumulative frequency of scratching bouts in male and female towhees. The model predicts linear relationships. (There is 1 data-point not shown for males at 13 scratches/bout; see text for fit of regression lines.)

where f_s is the frequency of bouts having s or more scratches (i.e., a cumulative frequency), p is the constant probability of uncovering food and B is the number of bouts observed. Equation (1) expresses a linear relationship between log f_s and $s - 1$, with slope log p (negative because p is fractional) and intercept log B, so that log f_s is inversely proportional to $s - 1$ and hence to s. We tested for linearity of the proportionality in both male and female towhees, thereby providing the first comparison of sexes within a species. In addition we experimentally tested the model by changing the probability, p, of uncovering food to see if the slope changed as predicted by eq. (1). The data consist of 381 scratching bouts (296 from males, 85 from females) observed by E.H.B. in Knoxville during the period 12 February to 29 March 1977, and 132 bouts (54 male, 78 female) by J.P.H. in Nashville on 25–27 December 1976. Both sets of data come from suburban lawns in the vicinity of feeding trays, with about 4 towhees present in the area in Knoxville and about 6 birds present in Nashville.

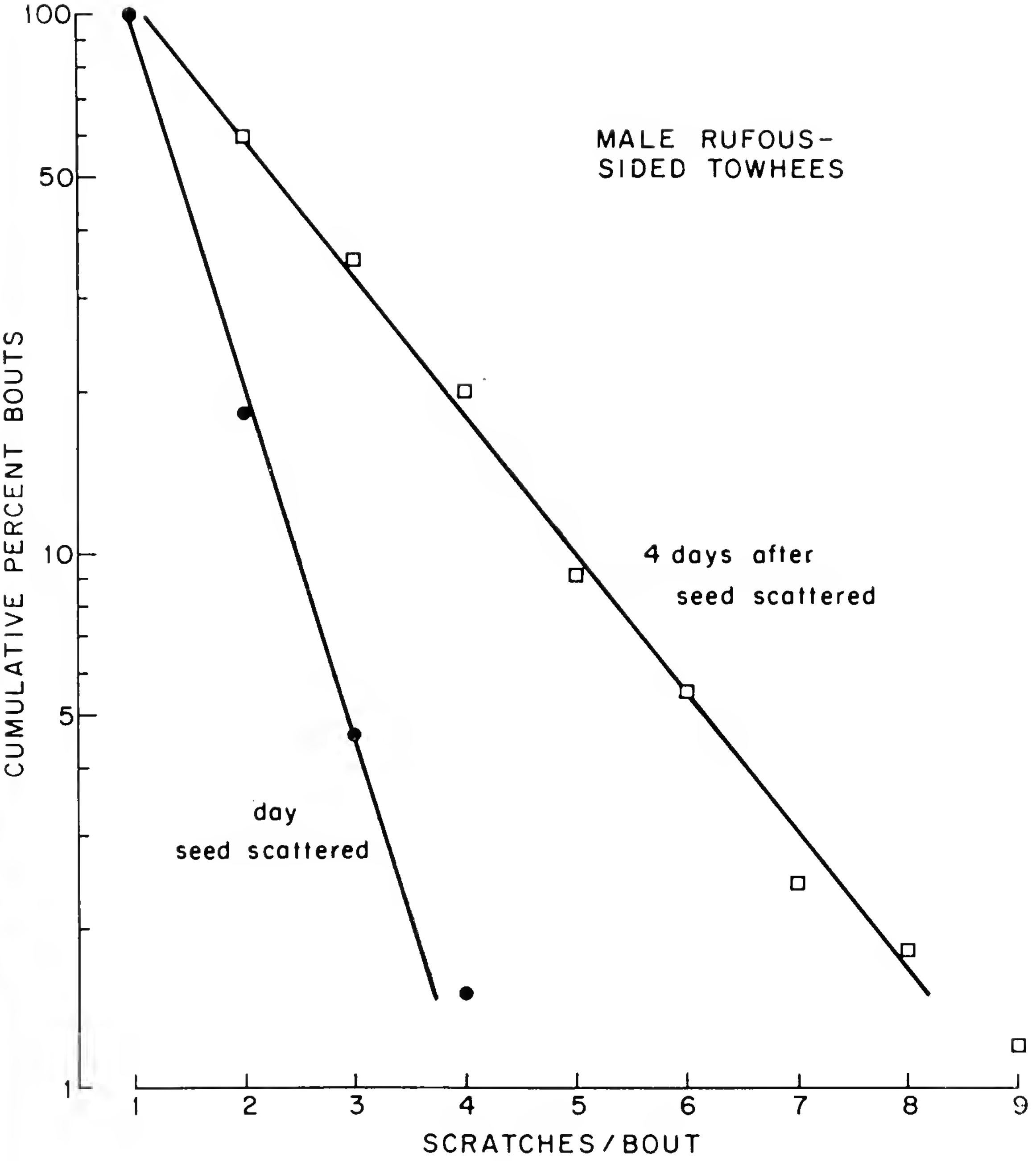

Fig. 2. Cumulative (normalized) frequency of scratching bouts in male towhees under 2 conditions of food-abundance. The model predicts a steeper slope on the day seed was scattered than 4 days afterward. (There is 1 data-point not shown at 13 scratches/bout for the right-hand curve; see text for fit of regression lines.)

Fig. 1, which plots all the data except 1 observation of a bout of 13 scratches by a male, shows that both males and females conform to the predicted linear inverse relation between number of scratches/bout and the cumulative frequency of bouts. The correlation coefficients for the total data are $r = -0.959$ for males and $r = -0.865$ for females. Cumulative frequencies have the annoying property of being much more reliable at higher values than at lower values, where random occurrences such as the 1 bout of

13 scratches by a male can cause considerable departure from linearity. Hence correlations are more meaningful when calculated from distributions that use cumulative frequencies above some arbitrary value that excludes random fluctuations at small sample sizes. When calculated on data $f_s \geq 5$ bouts, the correlation coefficients are much higher: $r = -0.996$ (males) and $r = -0.990$ (females). The least-squares regression lines shown in Fig. 1 were calculated from these data. The slight difference in slopes opens a new question concerning possible differences in foraging between the sexes.

The model of scratching was tested by changing the probability of finding food. Because p in eq. (1) is a fraction, its logarithm is a negative number (hence the slope of Fig. 1 is negative). Reducing the probability of finding food should produce a flatter slope (more scratches/bout), and this prediction was tested by comparing scratching of males on the day seed was scattered ($N = 131$ bouts) and 4 days after ($N = 165$ bouts). The data were normalized to 100% for ease in comparison of the slopes, and are plotted in Fig. 2. As predicted, male towhees show more scratches/bout when food is less abundant. Based on $f_s \geq 5$ bouts, the correlation coefficients are $r = -0.998$ for both sets of data, and regression lines are fitted to these data. The slopes may be conveniently expressed as half-lives (equal to the medians), which are 1.4 scratches/bout on the day seed was scattered and 2.3 scratches/bout 4 days after providing seed. Data on females showed the same direction of difference, but are too few to merit formal analysis.

The model may have application to foraging behavior of other species, and is now sufficiently tested comparatively for emberizine scratching to be a useful tool in behavioral ecology. J.P.H. has begun experiments from which preliminary data indicate that a heavier leaf-litter also shifts the distributions to greater scratches/bout, suggesting that p is dependent both upon the abundance of food and the amount of litter in which it is concealed. These easily recorded data, especially if combined with measures of scratching per unit time, could therefore serve as a powerful quantitative measure of foraging efficiency for comparing individuals, sexes, habitats, seasons and so on.—EDWARD H. BURTT, JR., *Dept. of Psychology, Univ. of Tennessee, Knoxville, TN* (Present address: *Dept. of Zoology, Ohio Wesleyan Univ., Delaware, OH 43015) and* JACK P. HAILMAN, *Dept. of Zoology, Univ. of Wisconsin, Madison, WI 53706.* *Accepted 29 Dec. 1977.*

Wilson Bull., 91(1), 1979, pp. 126–131

Winter diet of a bark-foraging guild of birds.—Although the literature of economic ornithology is replete with qualitative descriptions of the food habits of various birds, quantitative assessment of avian diets is seldom presented (Hartley, Ibis 90:361–381, 1948). For modern ecological analysis, earlier data reported in the literature are often inadequate for any one of several reasons. Birds were usually collected over large geographic regions, and therefore, fine scale comparisons are impossible. Evaluations of stomach contents were usually only subjective estimates; therefore, quantitative comparisons among species may not be reliable. Diets were often reported for the entire year; thus, few seasonal comparisons can be made. Here we report a quantitative analysis of the diets of bark-foraging birds which coexist in central Illinois during winter. The species include Red-headed Woodpecker (*Melanerpes erythrocephalus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Downy Woodpecker (*Picoides pubes-*

cens), White-breasted Nuthatch (*Sitta carolinensis*), and Brown Creeper (*Certhia familiaris*).

We collected Red-headed Woodpeckers during December through February, 1974–75 and 1975–76, and other birds during December through February, 1975–76, from upland deciduous forests in central Illinois. Almost all areas were adjacent to land used for agriculture. The dominant trees of our sites were white oak (*Quercus alba*), red oak (*Q. rubra*), black oak (*Q. velutina*), and shagbark hickory (*Carya ovata*). After collection, we immediately injected the birds with a formalin solution or placed them in an ice chest to insure curtailment of digestion (Koersveld, Proc. 10th Int. Ornithol. Congr., 1951).

Prior to quantification, all stomachs were opened and the contents identified. Stomach contents were then placed in a petri dish and food items identified at 50 random points for each sample. Because food items do not all break into the same sized pieces, frequency of points does not necessarily represent volume of diet. Volumetric determinations, however, were not possible because of the small size of many of the food items. A complete list of the families of insects identified is given in Williams (Ph.D. Thesis, Univ. of Ill., Urbana, 1977).

Numbers of insects in each sample were quantified by counting head capsules or wings (divided by 2). Since it was impossible to ascertain the number of some seeds, we used the frequency of occurrence in point samples as an indication of number. This assumes that large and small seeds break into a similar number of parts. Since large seeds appear to break more, this procedure overestimates numbers of large seeds. We determined sizes of insects by placing parts together and sizes of seeds from a reference collection. Data were then combined to give frequency of occurrence of each food size in the diets of the birds, and mean food sizes were calculated.

We are cognizant of problems inherent in any gut content analysis such as differential digestion rates (Mook and Marshall, Can. Entomol. 97:1144–1149, 1965). Since we failed to keep members of this guild alive in captivity and thus could not perform experiments on digestion rates, we deem stomach content analysis the best estimate of relative proportions of food items in their diets until further experimentation.

Our results indicate that Red-headed Woodpeckers consumed acorns during a winter with good mast crops (1974–75), but foraged more on corn and other seeds when mast crops were low (Table 1). Most of the arthropods taken were adult beetles.

The diet of the Red-bellied Woodpecker also contained mostly vegetable material (Table 1). Mast was relatively unavailable during the winter of 1975–76, and these birds foraged mostly on corn and other seeds. Two Red-bellied Woodpeckers collected 15 November 1976 when mast was abundant (not included in Table 1), had eaten 70% acorns, suggesting that this species may also prefer acorns when available. Most of the remaining items were adult beetles. Considering the difference in sample size, diets of these 2 species were remarkably similar in 1975–76. Differences were not significant for percent animal and vegetable foods taken but were significant (χ^2, $P < 0.05$) for the categories in Table 1.

Downy Woodpeckers consumed relatively more insects than the previous 2 species (Table 1). Ants, adult beetles, and small homopterans composed the bulk of the animal food. In addition, some larvae, especially from wood-boring families, were found. Vegetable foods consisted mostly of corn, poison ivy seeds (*Rhus radicans*), and some mast.

White-breasted Nuthatches were mainly vegetarian during winter (Table 1), but less so than Red-headed and Red-bellied woodpeckers. Seeds such as corn, acorns, wheat

TABLE 1

RELATIVE FREQUENCY (PERCENT) OF EACH FOOD CATEGORY FOUND IN STOMACHS OF BARK-FORAGING BIRDS DURING WINTER

Category	Red-headed[1] (N = 21)	Red-headed[2] (N = 6)	Red-bellied[2] (N = 20)	Downy[2] (N = 20)	White-breasted Nuthatch[2] (N = 20)	Brown Creeper[2] (N = 5)
Orthoptera	—	—	0.3	0.1	2.9	—
Hemiptera	0.2	—	—	3.4	3.0	22.8
Homoptera	—	—	0.3	7.6	0.3	34.4
Coleoptera (adults)	2.2	3.3	4.0	15.9	6.5	12.4
Coleoptera (larvae)	—	—	—	4.2	—	—
Lepidoptera (larvae)	—	—	—	1.4	2.7	—
Diptera (larvae)	—	—	—	0.6	—	—
Hymenoptera (adults)	1.1	—	0.8	20.7	7.2	4.4
Hymenoptera (larvae)	—	—	—	0.6	1.1	—
Araneida	0.2	1.2	—	4.5	1.0	11.6
Other	—	—	—	0.3	0.2	2.8
Unknown	0.2	—	0.6	1.8	3.3	3.6
Total Animal	3.9	4.5	6.0	61.1	28.2	92.0
Mast[3]	51.6	14.6	8.8	5.1	6.6	2.0
Zea mays	41.8	67.3	70.9	19.7	49.7	5.6
Helianthus sp.	0.1	—	—	0.4	5.5	—
Crataegus sp.	—	—	0.6	—	0.3	—
Triticum aestivum	0.1	—	—	2.0	5.7	—
Vitis sp.	—	6.3	9.4	1.7	0.1	—
Rhus radicans	0.2	—	—	7.1	—	—
Celtis occidentalis	—	—	2.4	—	—	—
Cornus sp.	—	5.5	—	—	—	—
Other	—	—	—	0.1	0.1	—
Unknown	2.3	1.8	1.9	2.8	3.8	0.4
Total Vegetable	96.1	95.5	94.0	38.9	71.8	8.0
Grit[4]	+	+	+	−	+	−

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[1] Birds collected during a relatively high mast year (1974–75).
[2] Birds collected in a low mast year (1975–76).
[3] Mostly *Quercus* sp.
[4] Indicates presence or absence of grit in stomachs examined.

TABLE 2

NICHE BREADTHS AND NICHE OVERLAPS FOR FOOD USE AMONG BARK-FORAGING BIRDS

	Food Breadth		Food overlap	C.D.*
RH (1974–75)	.05	RH × RB	.86	1.06
RH (1975–76)	.05	RH × DW	.29	1.63
RB (1975–76)	.04	RH × WBN	.62	1.62
DW (1975–76)	.30	RH × BC	.13	2.08
WBN (1975–76)	.11	RB × DW	.32	1.72
BC (1975–76)	.17	RB × WBN	.65	1.71
		RB × BC	.14	2.20
		DW × WBN	.49	1.01
		DW × BC	.42	1.23
		WBN × BC	.27	1.29

* C.D. = Character Difference, i.e., the ratio of larger bill length to shorter. Symbols represent species of guild.

(*Triticum aestivum*), and sunflower (*Helianthus* sp.) comprised most of the vegetable diet. Insects taken were mostly adult beetles, small bugs, adult orthopterans (Acrididae), and lepidopteran larvae.

Brown Creepers foraged more on insects during winter (Table 1) than any other guild member. Small homopterans (usually Psyllidae) and hemipteran insects were most frequently identified. Other significant prey items included beetle adults, spiders, and ants. For vegetable foods, Brown Creepers ate only small quantities of corn and acorns. The diets of all species were significantly different from one another (χ^2, $P < 0.05$).

Niche breadth values (Levins, Evolution in Changing Environments, Princeton Univ. Press, Princeton, N.J., 1968) for diet (categories of Table 1) indicate that guild members can be ranked from most to least specialized as follows: Red-headed and Red-bellied woodpeckers; White-breasted Nuthatches and Brown Creepers; and Downy Woodpeckers (Table 2). Species which concentrated on vegetable resources were the most specialized. Previously Williams (Am. Midl. Nat. 93:354–367, 1975) adduced that Downy Woodpeckers are generalists compared to other guild members. Data presented here lend credence to this hypothesis.

Because of their behavioral and morphological similarity, Red-headed and Red-bellied woodpeckers have recently been placed in the same genus (Mayr and Short, Publ. Nuttall Ornithol. Club, No. 9, 1970). Dietary overlap patterns further point out the similarity between these species and suggest that they are potentially strong competitors (Table 2). Elsewhere, we have hypothesized that these species exploit many resources in common during winter and that horizontal separation into different habitats permits coexistence (Williams and Batzli, Condor in press). These data augment our previous contention.

We found a correlation between mean food size and bill length among bark-foraging birds in central Illinois (Fig. 1). Body weight was also positively correlated with mean food size ($r^2 = .74$, $P < 0.02$). Larger birds tended to consume larger prey items.

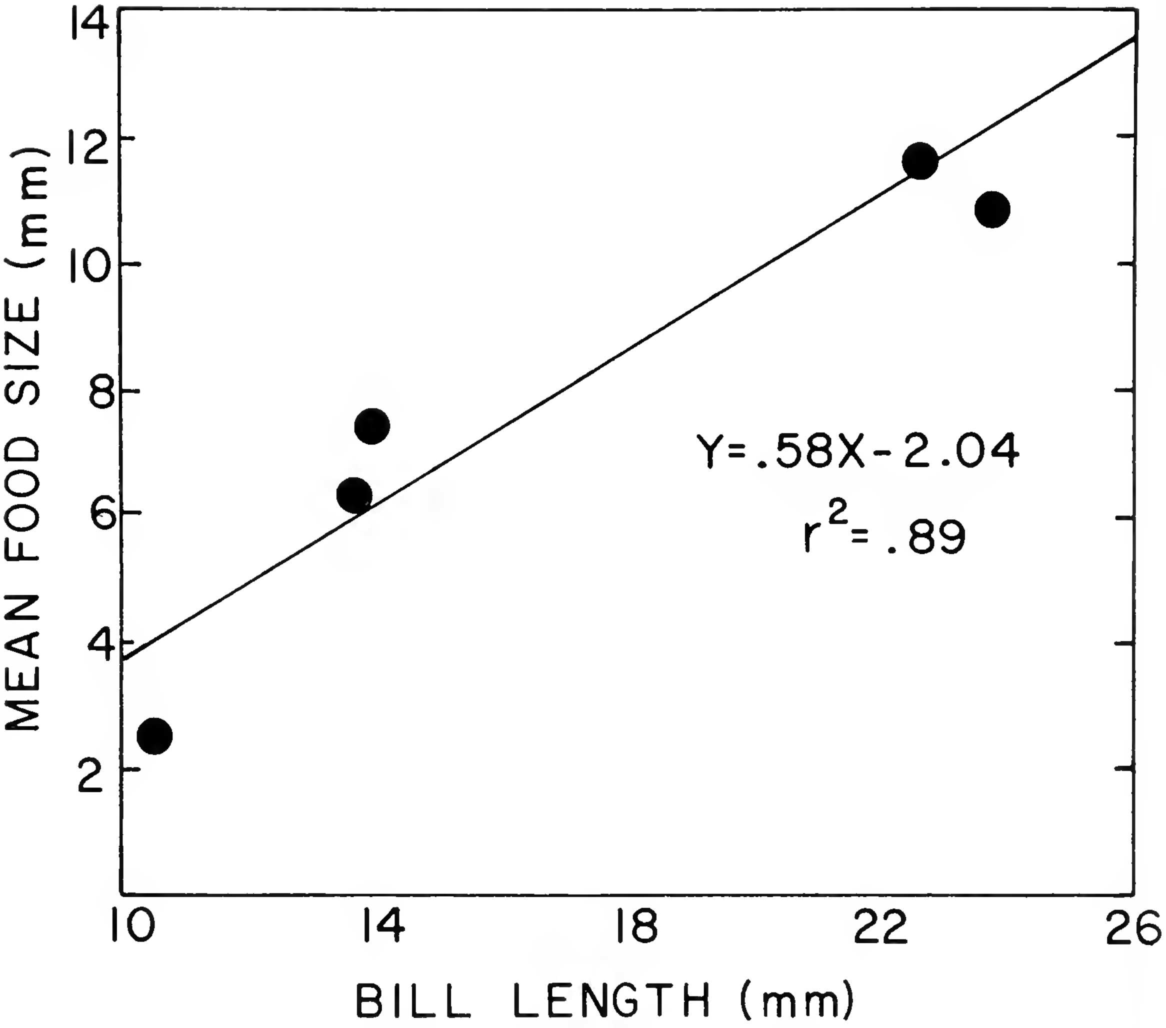

FIG. 1. Relationship between mean food size and bill length in bark-foraging birds in central Illinois during winter. Bill size for each species was RH = 22.6 ± 0.3 mm (1 SE), RB = 23.9 ± 0.3 mm, DW = 13.9 ± 0.1 mm, WBN = 14.0 ± 0.1 mm, and BC = 10.9 ± 0.2 mm. The slope was significantly different from zero ($P < 0.01$).

Several authors have used differences in culmen length to estimate the degree of niche overlap in birds (e.g., Schoener, Evolution 19:189–213, 1965). In the bark-foraging guild, we found a weak negative correlation between ratios of culmen length (large to small) and diet overlap ($P = 0.05$, $r^2 = .42$). We point out, however, that single comparisons should be made with caution, especially for interfamilial comparisons. For example, the relatively high C.D. (Table 2) for Red-headed Woodpeckers and White-breasted Nuthatches would not accurately predict the dietary overlap between these species. If White-breasted Nuthatches were collected during a winter of high mast availability, we suspect dietary overlap with Red-headed Woodpeckers would be even greater. Determination of diet overlap for Downy Woodpeckers and White-breasted Nuthatches from C.D. values would also be problematical.

Hespenheide (Ibis 113:59–72, 1971) indicated that food size is an increasing function of body size among some bird species. Our results generally agree with his findings. Bill length was the best predictor of food size, but bill length and body size were highly correlated. Food size for this guild may reflect the type of food which the birds must take in order to meet their energetic requirements.

E. Macleod, J. Bouseman, G. Godfrey, and J. Sternburg helped with insect identification. R. W. McFarlane, J. P. Skorupa, and an anonymous reviewer made helpful suggestions on an earlier draft.—JOSEPH B. WILLIAMS AND GEORGE O. BATZLI, *Ecology Program and Dept. of Ecology, Ethology and Evolution, Univ. of Illinois, Urbana, IL 61801.* (Present address of JBW: *Dept. Natural Science, Pepperdine Univ., Malibu, CA 90265*). *Accepted 9 Jan. 1978.*

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Mantids selected as prey by Blue Grosbeaks.—I observed Blue Grosbeaks (*Guiraca caerulea*) at their nests in Hawkins County in upper eastern Tennessee to feed their nestlings on mantids almost exclusively. Two active nests 1.65 km apart were photographed from blinds, each over a period of 3–4 consecutive days. Observations began on 29 June and 5 July 1977 when the nestlings were approximately 1 day old. In addition Rick A. Phillips and I observed 3 other nesting pairs of grosbeaks while they were feeding nestlings at sites 1.0, 9.7, and 38.7 km from the 2 photographed nests. The behavior of the adult birds was essentially the same at all nests in over 100 observed feedings.

Almost all the mantids these birds were gathering were very large, in excess of 75 mm, and were probably the introduced Chinese Mantid (*Tenodera aridisolia*). The head and wings had been removed from all the carcasses as had all, or most, of the legs before the insect was brought to the nest-site. This 1 food was almost the exclusive prey item (greater than 96%) brought to the young at all nests observed. The only other known food presented was an occasional grasshopper.

Males showed no strong tendency to feed and were easily discouraged by the sounds of the camera and strobes, often eating the food they carried. Females seemed little disturbed by the photographer's activities once I was concealed in the blind. They fed more often than the males, averaging 3–5 trips to each made by the male (if the male was feeding the young at all). Frequency of feeding depended, at least in part, on how far the birds went from the nest to gather food and how quickly they found it once there. Usually they would return to the same area in which the previous insect was taken upon completing a feeding. Mantids were brought to the nest as often as 5–10 min apart, but the average time between feedings was approximately 25–30 min. Most active feeding periods were the first 3 h after daylight and the last 2 h before dark. There were periods in each day when both birds would be absent from the nest and out of sight of the observer for more than an hour followed by intense activities of feeding the young.

The methods used by Blue Grosbeaks to catch mantids consisted principally of 1 or both birds flying to a weed-top perch and sitting motionless for a few seconds. The birds then either made low short flights and hovered over or adjacent to the weedy vegetation, plucking the insect from the leaves and stems, or flew to the ground and hopped among the grasses until a capture was made. The male often followed the female from place to place as she hunted and accompanied her return to the nest though not having made a kill himself.

The most common large insect in the fields where these birds were feeding were grasshoppers. These invertebrates, ranging in size from 20 mm to approximately 50 mm, were abundant in the vegetation—many jumped and flew from underfoot in all directions as I walked through the birds' nesting and feeding areas. This orthopteran is reported by McAtee (1908, *in* Bent, U.S. Natl. Mus. Bull. 327, 1968) as the most important element of the animal food eaten by this species and comprises more than 74% of the food fed to the young. The mantid's large size (most were 75–100 mm and some were in excess of 100 mm), in addition to their slow movements and their tendency to remain motionless when approached must make them most desirable to grosbeaks. Blue Grosbeaks in upper eastern Tennessee are exploiting a food source for which I find no previous record in the literature.—Fred J. Alsop, III, *Dept. of Biology, East Tennessee State Univ., Kingsport Univ. Center, University Blvd., Kingsport, TN 37660.* *Accepted 7 Feb. 1978.*

Wilson Bull., 91(1), 1979, pp. 132–133

Red fox predation on Greater Sandhill Crane chicks.—At the Malheur National Wildlife Refuge in Oregon, Littlefield (Proc. Int. Crane Workshop, Baraboo, Wis., 1976: 86–92) established the coyote (*Canis latrans*) as a predator on Sandhill Crane (*Grus canadensis*) chicks. He recorded heavy losses of Sandhill Crane young to coyotes in 1973 and 1974 during a low point in black-tailed jackrabbit (*Lepus californicus*) populations. Walkinshaw (The Sandhill Cranes, Cranbrook Inst. Sci., 1949), however, reports having searched many red fox (*Vulpes fulva*) dens located near Sandhill Crane nests without finding any crane remains. During the spring of 1977 we observed 2 instances of red fox predation upon Greater Sandhill Crane chicks (*G. c. tabida*) in southeastern Wisconsin.

On 15 May 1977 Drieslein discovered 2 freshly killed Sandhill Crane chicks at an active red fox den within the Horicon National Wildlife Refuge in Dodge County, Wisconsin. The chicks were lying at an entrance to a den where 3 fox pups had been observed on several occasions earlier in the week. Both chicks had been bitten in the back and neck, and judging from their fresh appearance, they were probably killed that same day. Based on growth curves developed for captive Sandhill Cranes, the chicks were between 3 and 5 days old (Ron Sauey, pers. comm.).

On 22 May 1977 Bennett was observing a pair of Sandhill Cranes and their 6-day-old chick with a 60× spotting scope at a distance of 200 m. The birds were feeding in a 2 ha field of short grass surrounded on 3 sides by shrubs in northern Green Lake County, Wisconsin. At 07:10 a red fox approached from an adjacent field and disappeared into a row of shrubs at the edge of the field where the cranes were feeding. The cranes were visually screened from the fox and did not appear to be aware of his presence. At 07:20 the fox reappeared on a wooded ditch bank directly in line with the cranes at a distance of about 30 m. For the next 15–20 min, the fox remained partially concealed and motionless while the cranes continued feeding along the edge of the ditch. At 07:40 the fox ran toward the cranes, picked up the chick which was within 2 m of 1 adult, and continued running with the chick into the nearest shrubs. Both adult cranes had their heads down when the fox charged and did not react until it was within 6–8 m of the chick. Their initial response was a distraction display with each adult running in opposite directions with head and wings lowered. They continued this display for

10 min after their chick had been captured. The pair of cranes remained in the area for 1 week after the incident but the chick was never seen again.

These observations establish the ability of the red fox to prey on Sandhill Crane chicks up to 1 week of age. The extensive use of upland fields and wooded pastures as feeding sites by cranes with young chicks increases the opportunity for encounters with fox. In the case of Bennett's observation, the ability of the fox to surprise the cranes with a short run from cover was probably very important in his success. The normal distraction behavior of the adults afforded no protection in this situation. Although observations described here are chance encounters, we believe that fox predation may play a more important role than previously believed in the loss of young Sandhill Crane chicks in Wisconsin.

We are grateful to Ron Sauey, International Crane Foundation, Baraboo, Wisconsin, for aging the crane chicks, and Richard Hunt and Jack Toll for helpful suggestions and review of the manuscript.—Robert L. Drieslein, *Horicon National Wildlife Refuge, Route 2, Mayville, WI 53050, and* Alan J. Bennett, *College of Natural Resources, Univ. of Wisconsin, Stevens Point, WI 54481.* *Accepted 30 Nov. 1977.*

Wilson Bull., 91(1), 1979, p. 133

Owl predation on a mobbing crow.—On 29 November 1962, at 16:30 on an overcast afternoon in a hilly wooded area near Amherst, Virginia, I watched a flock of Common Crows (*Corvus brachyrhynchos*) mob a Great Horned Owl (*Bubo virginianus*). I was 200 m distant and had 7× binoculars. The loud cawing of the crows drew my attention. The owl was located 10 m up in a tree. The crows flew around the tree, dove at the bird, and perched on nearby branches, as they directed their vocalizations at the predator. After I had observed this activity for 5 min, the owl quickly extended its left foot and grasped a crow which had ventured within reaching distance. At this action, the cawing and diving became more frenzied. The owl held the crow in its talons and pinned it against its lower body and the limb for 30 sec. I didn't observe struggling from the crow. The owl still in possession of the captured bird then flew out of sight into the woods pursued by the noisy flock of crows.

Current thought views mobbing as relatively safe and of correspondingly low risk to those participating in the action. I am unaware of any examples in the literature which reference a mobbing bird actually falling prey to a predator during the mobbing event. This incident demonstrates the relativity of the current theory in relation to mobbing behavior.—Render D. Denson, *Dept. Biological Sciences, Box 5640, Northern Arizona Univ., Flagstaff, AZ 86001. (Present Address: Kramer, Chin and Mayo, Inc., 1917 First Ave., Seattle, WA 98101).* *Accepted 9 Dec. 1977.*

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Ruddy Turnstones destroy Royal Tern colony.—The Ruddy Turnstone (*Arenaria interpres*) occasionally eats eggs of other birds. Parkes et al. (Wilson Bull. 83:306–308, 1971) summarized 3 reports of such behavior by the Old World subspecies (*A. i. interpres*) and presented 2 instances involving the New World subspecies (*A. i. morinella*). We report here a seemingly extreme instance of this behavior.

In May and June of 1977, we observed the large scale destruction by turnstones of eggs laid in a large colony of Royal Terns (*Sterna maxima*) at Bird Island and Little Bird Island in Nassau Sound, Duval Co., Florida, and the subsequent abandonment of the colony by the terns. The terns had nested successfully here in most years since the late 1950's (Sam Grimes, pers. comm.). This was the fourth year of our studies in this colony and the first time we observed the turnstone behavior.

On 15 May, Sutton found Royal Terns making a strong start toward the establishment of their annual colony. The first subcolony (A) had 282 eggs and was well tended. Adults were typically calm, allowing close approach before flushing. Returning birds landed and calmed down quickly. Indications were that the colony was off to a good start and would continue to build up to about 2000 nests as it did in 1976.

On 20 May, we found subcolony A abandoned; 20% of the eggs were broken and many of the remainder were partially buried or rolled together in groups. Two new subcolonies (B and C) had been started about 100 m west, each contained about 150 eggs. It was apparent from the actions of the birds that they were under stress. They flushed when observers were far from the colony and did not remain in groups directly over the colony as is normal. Both subcolonies contained some broken and some partly buried eggs, indicating abandonment or improper care by adults. The birds did not return while we were in a blind about 20 m away. This was unusual. When we retired to a greater distance, they returned with much hesitation, flushing repeatedly before settling down.

On 22 May, the situation was as follows: subcolony B still contained about 40 eggs intact, but many others were freshly broken; subcolony C was gone and broken egg shells littered the area; and a new subcolony (D) containing 50 eggs had been started on Little Bird Island, 0.5 km to the west. We decided to make further observations with binoculars from a distance of about 200 m. After the royals had returned and settled down on subcolony B, we saw a small group of Ruddy Turnstones enter the colony and begin pecking at eggs. To confirm that these birds were actually breaking the eggs, we cleared the area of all shell fragments leaving 36 perfect eggs. After we retired and the royals had returned and settled down, 6 Ruddy Turnstones and 2 Sanderlings (*Calidris alba*) entered the colony and began to peck at the eggs, breaking them open and feeding on them. After about 30 min we again entered the colony and found 6 broken eggs. We did not see Sanderlings actually breaking eggs, they may well have been simply feeding on eggs broken by the turnstones.

The turnstones apparently broke eggs at a devastating pace. They dashed about in the colony almost in a frenzy, breaking an egg open, snatching a mouthful, dodging a lunge from a royal, and then pecking at another egg. Between 09:00 20 May, and 09:00 22 May about 260 eggs were broken at subcolonies B and C (30 h of daylight). This is about 8.7 eggs per daylight hour. During the 30 min observation period on 22 May, 6 eggs were broken by 6 turnstones, but the colony had been cleared by us. With no broken eggs to feed on, the rate may have been somewhat higher than it would have been with many broken eggs. The turnstones did not break open an egg and then finish it before going on to another as reported with undefended eggs (Parkes et al., op. cit.). Thus the ineffectual defense of their eggs by the royals probably resulted in more destruction than no defense at all. Royal Terns are relatively unaggressive toward predators (Buckley and Buckley, Ibis 114:351, 1972). Those we observed did not seem to recognize turnstones as a threat, limiting the defense of their eggs to an occasional lunge. In contrast, on 12 June, Sutton observed a Herring Gull (*Larus argentatus*) steal an egg from a small colony of 4 Royal Tern nests on Bird Island. The terns reacted strongly, one chasing the gull out of the colony and actually striking it on the back.

On 30 May, we found no viable Royal Tern eggs on Bird Island. Subcolony D on Little Bird had grown to 688 eggs and had then been abandoned. We found another subcolony (E) of 98 eggs also abandoned with many broken eggs. Through June, the Royal Terns continued nesting attempts in small groups on both islands. They laid 76 eggs in 8 small subcolonies ranging in size from 2 to 26 eggs. All these were ultimately either broken or abandoned.

During our observations on 30 May, 22 Ruddy Turnstones were on the beach, but only 1 was seen feeding on broken eggs in abandoned subcolony D. This confirmed our suspicion that the turnstones were attracted to the densely packed mass of adult Royal Terns standing in the colony, rather than to the eggs themselves. During our observation period on 22 May, we twice observed that the turnstones did not enter the colony until after the royals had returned and settled down, even though they had an opportunity to attack the eggs when undefended. Once the royals abandoned the colony, most of the turnstones ignored it. After subcolony A was abandoned, scores of intact eggs lay completely unprotected for at least 7 days. In the meantime, turnstones were stealing eggs from subcolonies B and C where adult terns were still present. By contrast, in 4 of 5 cases discussed by Parkes et al. (op. cit.), turnstones were observed taking only undefended eggs.

Three other species had nests on the Bird Islands during this period. We found no Least Tern (*Sterna albifrons*) eggs broken in 200 nests, 7 Gull-billed Tern (*Gelochelidon nilotica*) eggs broken in 180 nests (3.9%), and 14 Black Skimmer (*Rynchops nigra*) eggs broken in 816 nests (1.7%). We did not see turnstones break these eggs, but we believe that they did. Gulls were probably not responsible as they usually remove eggs from the nest, rather than break them *in situ*. Least and Gull-billed terns are more aggressive toward predators than are Royal Terns, but whether they recognize turnstones as predators is not known. Of the 4 species, the royals seemed particularly vulnerable to turnstone predation because they lacked aggression, seemingly failed to recognize turnstones as predators, and tended to desert the colony en masse when disturbed (Buckley and Buckley, op. cit.).—ROBERT W. LOFTIN, *Univ. of North Florida, Box 17074, Jacksonville, FL 32216, and* STEVE SUTTON, *4419 Silverwood Lane, Jacksonville, FL 32207.* *Accepted 19 Jan. 1978.*

Wilson Bull., 91(1), 1979, pp. 135–137

Predation of black rat snakes on a Bank Swallow colony.—The Bank Swallow, *Riparia riparia*, is well known for its gregarious breeding colonies which usually are composed of clusters of burrows in riverbanks, cliffs and the like. Studies of these colonies have recently provided data useful for tests of the theoretical benefits of coloniality (Emlen and Demong, Science 188:1029–1031, 1975; Hoogland and Sherman, Ecol. Monogr. 46:33–58, 1976), and have demonstrated the potential benefits of breeding synchrony within the colony and group defense of eggs and young from predators. The basic assumption is that fitness of Bank Swallows in colonies must ordinarily be greater than might be expected if the swallows nested individually, otherwise coloniality would not continue indefinitely. I do not dispute this assumption, but I note there appears to be little information on failure or desertion of colonies due to predation. As it is obvious that such events sometimes occur, and because of the interest in the general benefits of coloniality, the following account of the apparent decline of a large Bank Swallow colony should be of interest.

For at least 25 years, Bank Swallows have nested on the James River near Presquile National Wildlife Refuge, Chesterfield Co., Virginia (Scott, Raven 29:122–123, 1958). Along with scattered colonies in nearby gravel pits (pers. obs.), this area represents 1 of only 3 known nesting locations for the species in Virginia (F. R. Scott, pers. comm.). Since early 1975, I have censused a large colony that has occupied the same section of riverbank for at least 8 years. This part of the James River is tidal and the riverbank containing the colony consistently erodes and falls away. Therefore, all burrows from the previous year are usually gone each spring. The section of bank occupied by the colony is about 300 m long, 3 to 5 m high and is composed of soil containing layers of sand or gravel. The swallows appear to prefer these layers for constructing their burrows. The bank is usually quite steep, but the amount of soil washing to the base of the slope varies from year to year depending upon water levels. During the study, I counted all burrows that appeared to have been completely excavated. Although I verified the existence of nests in many of these burrows, I could not reach others and made no overt attempts to do so as I wanted to avoid disturbing the colony. More than 300 individuals were banded and simple Lincoln-Peterson mark-recapture techniques (Brower and Zar, Field and Laboratory Methods for General Ecology, Wm. C. Brown, Dubuque, Iowa, 1976) were used to estimate the size of the colony each year.

In 1975, the colony was quite large (Table 1) and active. No predation was observed and the swallows appeared to be quite successful in producing young. River levels were fairly high that spring and the riverbank remained very steep, making access to the burrows difficult. In 1976, the colony again was large, even though an apron of slumped soil had begun to build up at the base of the riverbank. Late in that breeding season, when most burrows contained young that were near fledging, 3 black rat snakes (*Elaphe obsoleta*) were discovered in burrows. These snakes were obviously distended with swallows they had eaten and several young swallows were found dead in a burrow along with a live snake. These were apparently killed by the compression between the snake's body and the burrow wall. I removed the snakes and transported them some distance from the colony. In 1977, a considerable base had developed along the riverbank, and access to the burrows was greatly facilitated. The texture of the soil in the bank also appeared to have changed. The sand and gravel layers were nearly absent. Although the spring of 1977 was one of the warmest on record, Bank Swallows were late in nesting and the apparent size of the colony never reached 20% of former levels. Only 1 bird banded in previous years was captured, suggesting that alternate nesting areas were being used. Predation by black rat snakes was observed on 4 separate occasions. One snake captured from the colony contained 8 adult swallows. Another smaller snake contained 2 swallows, and at least 1 very large black rat snake was never captured, although it was observed in the colony and obviously had eaten several swallows. The snakes were mobbed whenever they emerged from the burrows, but there was little evidence that the mobbing was effective.

Ultimately the swallows moved the colony approximately 100 m upstream from the original site and began burrow construction. The nesting cycle was apparently interrupted as an egg was found in a burrow only a few cm deep (H. R. Laprade, pers. comm.). The second colony was subsequently abandoned in early June and to my knowledge no young were produced at this location. I suspect these birds moved to

TABLE 1

POPULATION DATA FROM A BANK SWALLOW COLONY NEAR PRESQUILE NATIONAL WILDLIFE REFUGE, CHESTERFIELD CO., VIRGINIA

Year	Number of burrows	Date of earliest activity	Number of adults	Number banded	Recaptures from previous years
1975	435	19 April	927	222	—
1976	388	24 April	875	87	15
1977	71	6 May	160	29	1

other colony sites in nearby gravel pits where they produced young, as postbreeding aggregations estimated at 1800 individuals were observed in late summer.

It is obvious that the location of Bank Swallow nests is a critical factor in the success of their reproduction. Failure of the present colony gives us evidence to apply to theories of some of the benefits of coloniality. First, I believe the desertion was largely due to the alteration of the structure and texture of the riverbank and/or subsequent increased predation by snakes. This supports the idea that coloniality is a response to localization of a critical resource, in this case appropriate nesting sites which are easily excavated and also inaccessible to most predators. It is possible that the swallows are proximately influenced by the physical nature of the cliff and fail to nest or abandon sites before intrusion by predators. The nesting attempts in 1977 may have been made by inexperienced birds born the previous season. This is supported by the lack of recovery of birds banded previously as adults. At any rate, mobbing appeared to be ineffectual in the defense of nest sites against the most common predator, the black rat snake, and only steepness of the riverbank seemed to discourage invasion by the snakes. It appeared to me that snakes were actively drawn to nest sites. Snakes may find nest sites as a result of their foraging activities along such areas, activities of the birds themselves, or olfactory attraction to snakes which previously had found the colony. If single snakes found the colony, predator-swamping would be of benefit, as individual snakes are capable of eating several swallows in a short period of time, but then would be no threat for several days. However, if the presence of a snake increases the probability of conspecifics locating the nest sites, as appears likely, this hypothesis becomes untenable.

I am indebted to H. R. Laprade and F. R. Scott for their original observations of Bank Swallows and to L. Blem and F. R. Scott for critically reading the manuscript. M. Banner, L. Blem, H. Laprade, R. Peer, and J. Steiner assisted in the field.—CHARLES R. BLEM, *Virginia Commonwealth Univ., Dept. of Biology, Academic Division, Richmond, VA 23284. Accepted 29 Dec. 1977.*

Wilson Bull., 91(1), 1979, pp. 137–141

Summer range and migration routes of Florida wintering Greater Sandhill Cranes.—Previously, Williams and Phillips (Auk 89:541–548, 1972) reported on sightings and recoveries of 169 Greater Sandhill Cranes (*Grus canadensis tabida*) banded and color-marked while wintering in northern Florida. Marking efforts have continued and recent reports have increased our knowledge of the summer range and migration patterns for cranes that winter in Florida.

In addition to the 169 cranes previously marked (Williams and Philips, op. cit.), 148 wintering cranes have been banded and distinctly color-marked from widely separated capture sites in Florida. One hundred and fourteen birds were captured on Paynes Prairie, Alachua Co. and 34 birds were captured on "KD Ranch" in southern Highlands Co. (Fig. 1A). Paynes Prairie is in the northern part of the Greater Sandhill Crane's winter range in Florida, and the Highlands Co. site is near the southern limit.

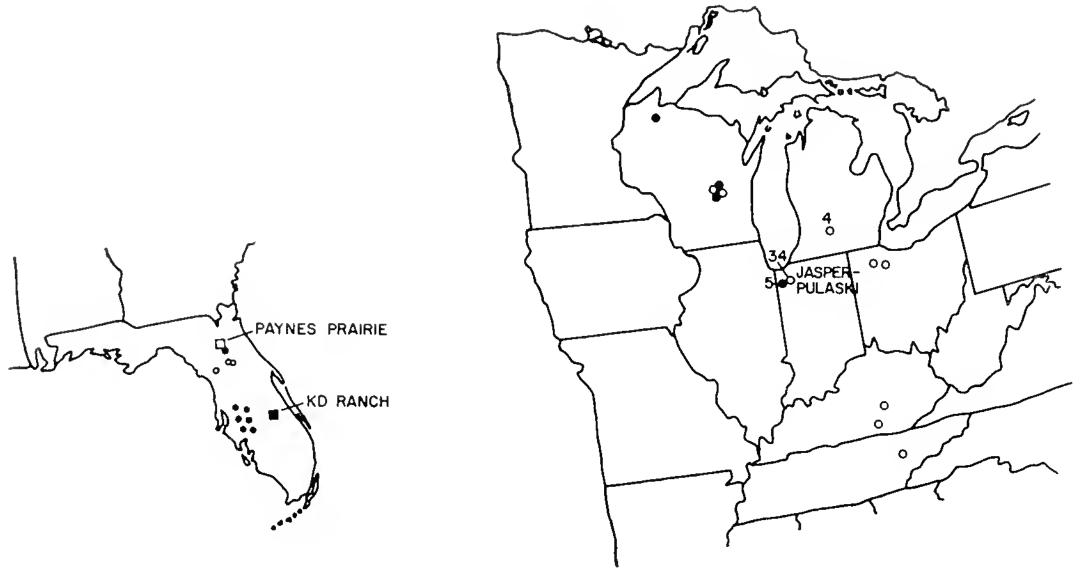
Since the 1972 accounting of Williams and Phillips (op. cit.), 150 marked cranes have been reported. The reports were grouped by season of observation and banding location (Fig. 1). Many of the sightings were from areas where cranes are known to concentrate during migration or where extensive fieldwork was being done and probably represent repeated sightings of the same individuals. An effort was made to eliminate re-sighting of the same individual birds during the same day, though in most cases, it was not possible to separate repeated sightings of an individual on subsequent days unless the bird was a member of a known pair.

The distribution of winter reports (Fig. 1A) shows dispersal of birds outside the general capture vicinity. Cranes wintering in south Florida were less likely to return to the same wintering areas than those using Paynes Prairie. Six of 34 birds banded in south Florida were re-sighted in subsequent years outside the capture area. Only 3 of 114 birds banded on Paynes Prairie were sighted outside the capture area. Loyalty to winter range probably is dependent on local land use practices and habitat conditions. The movement of the Paynes Prairie marked birds outside the general capture area occurred in 1975 and 1976 following changes in land use practices there (Nesbitt, Fl. Field Nat. 5:16–17, 1977).

Spring migration of cranes from Florida occurs between late February and early April with most birds leaving during early March (Nesbitt, Wilson Bull. 87:424–426, 1975). Reports of marked birds north of Florida were not numerous until they reached concentration points in southern Michigan (especially Jackson Co.) and at Jasper-Pulaski Fish and Wildlife Area in northwestern Indiana. Reports between northern Florida and these concentration areas usually resulted from band recoveries. Spring migration reports of northern Florida marked cranes (Fig. 1B) came from Tennessee (1), Kentucky (2), northwestern Indiana (34), and 2 birds were reported from Ohio. "KD Ranch" marked birds were reported during spring migration (Fig. 1B) from northwestern Indiana (5), central Wisconsin (2), and northern Wisconsin (1).

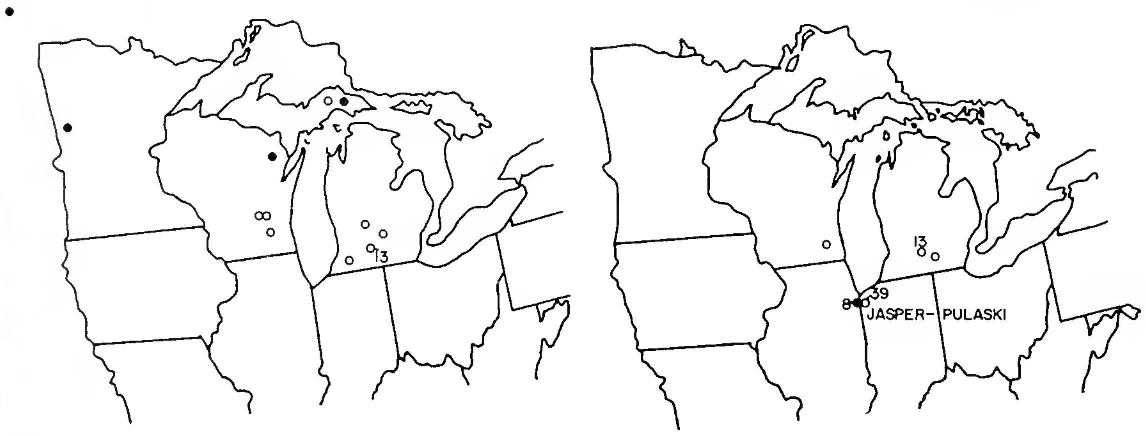
Summer records (Fig. 1C) of Paynes Prairie banded birds were concentrated in southern Wisconsin (3), southern Michigan (16), and 1 reported from northern Michigan. This is the same pattern reported by Williams and Phillips (op. cit.). Cranes banded in southern Florida were reported summering in northern Michigan (1), northern Wisconsin (1), Minnesota (1), and Manitoba (2) (Fig. 1C).

These data suggest differences in summering areas for cranes which winter at the 2 extremes of their range in Florida. Cranes banded in north Florida were reported summering in Michigan and southern Wisconsin while those banded at the southern end of their range were reported summering from northern Michigan and northern Wisconsin to Minnesota and Manitoba. At this time we have no information for the cranes breeding in Ontario.



A WINTERING REPORTS OUTSIDE CAPTURE AREA

B SPRING MIGRATION REPORTS



C SUMMER REPORTS

D FALL MIGRATION REPORTS

Fig. 1. Location of sightings of Greater Sandhill Cranes marked in Florida. Closed circles are birds captured at "KD Ranch." Open circles are birds captured at Paynes Prairie. (Exact location of sightings are available from the authors.)

Fall migration of cranes to Florida is more protracted than spring migration extending from September through December. The fall movement pattern (Fig. 1D) appears almost identical to spring migration with concentrations of birds again occurring in northwestern Indiana at Jasper-Pulaski and southern Michigan.

Cranes that winter in Florida and summer in Wisconsin, northern Michigan, Minnesota and eastern Manitoba concentrate during the fall and spring migration in northwestern Indiana at Jasper-Pulaski. Additionally, cranes that summer in Michigan and winter in northern Florida concentrate in southern Michigan, Jackson Co., during fall and spring migration. Walkinshaw (Wilson Bull. 72:358–384, 1960) suggested that these cranes fly from southern Michigan to Florida and do not concentrate again at the Jasper-Pulaski staging areas in Indiana. The 2 birds reported from Ohio and additional sight records in Ohio (Walkinshaw, op. cit. and Perkin, Sandpiper 9:5–7, 1966) substantiate

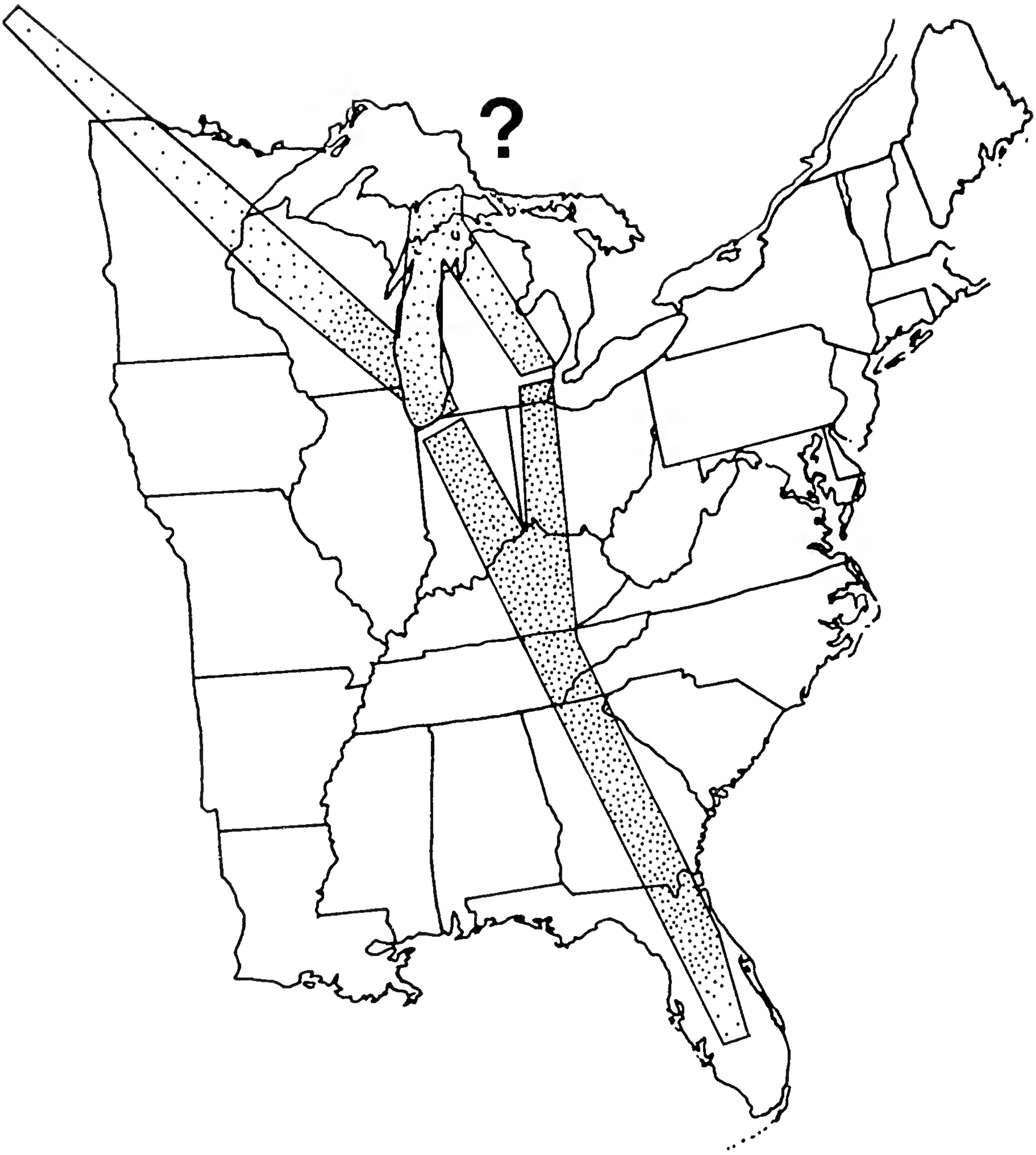


FIG. 2. Greater Sandhill Crane migration routes to and from wintering grounds in Florida.

the existence of a straight Michigan–Florida route. Numerous spring and fall reports of Sandhill Cranes over eastern Tennessee (Devore, The Migrant 43:29–34, 1972), Kentucky (Larson, Ky. Warbler 47:31, 1971; Maslowski, Ky. Warbler 44:57, 1968; Guthrie, Ky. Warbler 42:52, 1966) and Georgia (Walkinshaw, op. cit.; Fink, Oriole 31:12–13, 1966) further delineates the route used by cranes migrating to and from Florida (Fig. 2).

Except for overnight stops (Crete and Toepfer, U.S. Fish and Wildlife Serv. Mimeo. Rept., Twin Cities, Minnesota, 1978), spring and fall migration of cranes south of the northern Indiana and Michigan region is fairly direct with little extended stopping between those areas and Florida. The fact that no reports occurred between northern Indiana–southern Michigan and Florida during fall migration (0 of 62) while several (5 of 53) occurred during spring migration, suggests marked cranes migrating in spring are more likely to encounter adversities than when flying south in the fall. Williams and Phillips (1972) reported 1 spring observation and 2 fall observations between north Florida and the Great Lakes region.

The tendency for cranes summering in northern Michigan, northern Wisconsin, Minnesota, and Manitoba to winter principally in south-central Florida and cranes summering in Michigan (mostly the southern part of the state) and Wisconsin to winter primarily in north and central Florida, needs further study, especially the influences local habitat conditions have on wintering range in Florida.

We wish to express our appreciation to the many individuals who reported sightings of color-marked cranes. Principal among these were: G. Belyea, Mrs. M. Flagg, Mrs. M. Hall, R. Hoffman, W. Hummon, B. John, A. King, J. Lamendoler, J. Lasso, Mrs. J. Manita, S. Melvin, G. Nielsen, R. Rollo, D. Shroufe, D. Switzer, W. Taylor, H. Troth, H. Wing, R. Windingstad, and F. York. We also appreciate the help of W. J. D. Stephen in locating one of the Manitoba sightings. The manuscript benefited from the sound advice of J. C. Lewis and L. E. Nauman. We thank the Division of Recreation and Parks, Florida Department of Natural Resources for permission to trap on Paynes Prairie.

This study was part of a Federal Aid to Wildlife Restoration Program, Florida Pittman-Robertson Project W–41.—STEPHEN A. NESBITT AND LOVETT E. WILLIAMS, JR., *Wildlife Research Laboratory, Florida Game and Fresh Water Fish Commission, 4005 S Main Street, Gainesville, FL 32601.* *Accepted 21 Mar. 1978.*

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Olfactory guidance of Leach's Storm Petrel to the breeding island.—This report presents the first experimental evidence for olfactory navigation in Leach's Storm Petrel (*Oceanodroma leucorhoa*) during the terminal approach to a breeding island. Colonies of this species are found on 5 islands of the 200 km^2 Grand Manan Archipelago in the Bay of Fundy. Nest burrows in the larger colonies on Outer Wood, Hay, and Kent Islands are predominantly found under a thick canopy of spruce (*Picea* spp.), balsam fir (*Abies balsamea*), and mountain ash (*Sorbus americana*).

Like most other small procellariiforms, Leach's Storm Petrels typically arrive and depart from their colonies only in darkness, generally between 22:30–23:00 and 04:00–04:30 during the summer months at Kent Island. Visual cues alone seem insufficient for the birds to find and distinguish among the islands since arrival is not retarded under heavy cloud cover or in thick fog. Gannet Rock light, 2 km south of Kent Island, might be a useful reference to the general vicinity when visibility is not unduly impaired by fog. Sound cues likewise seem inadequate for use by the petrels. Thousands of Herring Gulls (*Larus argentatus*) nest on Kent Island, but their vocalizations, normally few and muted after dark, virtually cease on murky, foggy nights. Because gull colonies are also found on other islands of the archipelago, gull noises alone would not serve to distinguish a particular island in any case.

One potential navigational cue of value to the birds might be the distinctive, musky odor of petrels which is apparent to the human nose at considerable distance. Bang (Acta Anat. 65:391–415, 1966), Stager (Am. Zool. 7:415–419, 1967) and others have

TABLE 1

INFLUENCE OF WIND DIRECTION ON APPROACH DIRECTION OF LEACH'S STORM PETRELS TO THE EAST AND WEST COASTS OF THE BREEDING ISLAND

	Time after sunset of first call		Number of birds seen within 15 min after the first call	
Date	Upwind approach	Downwind approach	Upwind approach	Downwind approach
5 July 1970	–	94 min	–	0
12 July	111 min	–	10	–
19 July	103 min	–	49	–
23 July	–	103 min	–	0
4 August	–	105 min	–	0
			59	0

put forward the previously untested hypothesis that procellariiforms may use the odor of their breeding islands to locate them after dark. If Leach's Storm Petrels follow a wind-borne odor trail to Kent Island as they do to cod liver oil at sea (Grubb, Nature 237:404–405, 1972), one should be able to predict their direction of approach each night in terms of wind direction.

Use of an Image Intensifier Scope (Varo, Inc., Garland, Texas) allowed me to monitor incoming birds visually. This instrument creates an image by magnifying ambient light intensities electronically, thus avoiding phototaxic complications. As darkness approached, I placed the tripod-mounted scope upwind or downwind (randomly assigned) on either the east or the west side of the island's north end petrel breeding colony. After the instrument had been focused at 100–150 m and aimed out to sea in line with the wind, it was elevated so the ocean surface approximated a chord of 1.5 radii across the lower image field. For 15 min after the first call from a petrel in flight, I tallied birds coming to the island.

Differences in numbers of petrels flying to the colony up- or downwind were dramatic (Table 1; $\chi^2 = 88.5$, $P < 0.01$). In 2 trials totalling 30 min, 59 birds were watched coming to the colony from the leeward side(upwind), while none was seen flying with the wind toward the colony in 3 trials totalling 45 min.

The petrels approached, singly or in groups of 2 or 3, at estimated altitudes of 20–25 m, much higher than the average 1–2 m heights of birds foraging at sea. Incoming birds maintained these elevations until near the shoreline, then descended to tree top level (8–10 m) while passing in over the colony. Possibly due to the headwind, their rather direct approaches seemed to lack the gliding component displayed when foraging at sea. Limitations on Intensifier Scope sensitivity precluded observation under foggy or cloudy conditions.

Procellariiforms characteristically commute great distances between nesting colonies and feeding grounds. Breeding Slender-billed Shearwaters (*Puffinus tenuirostris*; Green, Emu 65:226, 1966) and Manx Shearwaters (*P. puffinus*; Lockley, Shearwaters, Doubleday, Garden City, New York, 1961) are known to feed over 800 km from their nests. Homing experiments (Griffin, Auk 57:61–74, 1940; Billings, Auk 85:36–43, 1968) disclose that Leach's Storm Petrels have the ability to return to Kent Island from release points hundreds or thousands of kilometers away. These release points must be far beyond the range of colony odor. Navigation must be based on senses other than olfaction, therefore, until the petrels get within the general vicinity of their breeding island. The use of olfactory cues, suggested by the upwind approach patterns to Kent Island, probably operates only within a few tens or perhaps hundreds of kilometers of the breeding site.

This note is based on part of a thesis submitted to the Department of Zoology, University of Wisconsin, in partial fulfilment of the requirements for the Ph.D. degree. I deeply thank John T. Emlen, Jr. for encouraging and critically evaluating this work. Charles E. Huntington provided logistic support at Kent Island and Helmut K. Buechner facilitated loan of the Image Intensifier from the U.S. Armed Forces. I thank Spencer G. Sealy and David B. Wingate for improving an earlier draft. This research was supported by a NIMH fellowship and by grants from the Frank M. Chapman Memorial Fund and the Society of the Sigma Xi.—THOMAS C. GRUBB, JR., *Dept. of Zoology, Univ. of Wisconsin, Madison, WI 53706* (Present address: *Dept. of Zoology, The Ohio State Univ., Columbus, OH 43210*). *Accepted 30 Nov. 1977.*

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Effects of highways on Red-winged Blackbird and Horned Lark populations.—Human disturbances that alter the distributions of wildlife populations through habitat modification are widespread. One example is highways, which directly affect wildlife populations in the right-of-way area, but may also have important effects in adjacent areas.

We conducted bird censuses along county roads and interstate highways in central Illinois during 1976 to test the efficacy of several census techniques. Transects perpendicular to the road, 100 m wide and 500 m long, were divided into 100 × 100 m blocks. Clusters of transects were located at random along interstate and county roads in Champaign County, Illinois. All transects discussed here were in fall-plowed fields planted to row crops (mostly corn and soybeans). Censuses were completed before crops matured. Census protocols included 4 and 8 min random walk and 4 min straight walk counts. For random walk counts the observer spent 4 or 8 min in each plot and walked throughout the plot as seemed appropriate to obtain a count of the birds. The observer walked the center line of the transect, spending 4 min in each plot, for straight walk counts. Transects did not include any pavement or gravel shoulder areas.

Census data are partitioned into 2 periods: late winter–early spring (10 Feb.–11 Apr.) and late spring (25 May–20 June). Census times were distributed from 30 min before to 4 h after sunrise. Eighty-six bird counts (62 early, 24 late) were made on 18 different county road transects and 69 (61 early, 8 late) were made on 15 different interstate highway transects. The same census technique was used on all plots within a transect on a given day and separate records were kept of each of the 5 1-ha blocks along the transect. Thus, comparisons of data from blocks at different distances from the highway yield some insight into the effect of highways on bird distributions.

Although data were collected on a number of species, only Horned Larks (*Eremophila alpestris*) and Red-winged Blackbirds (*Agelaius phoeniceus*) were common enough to

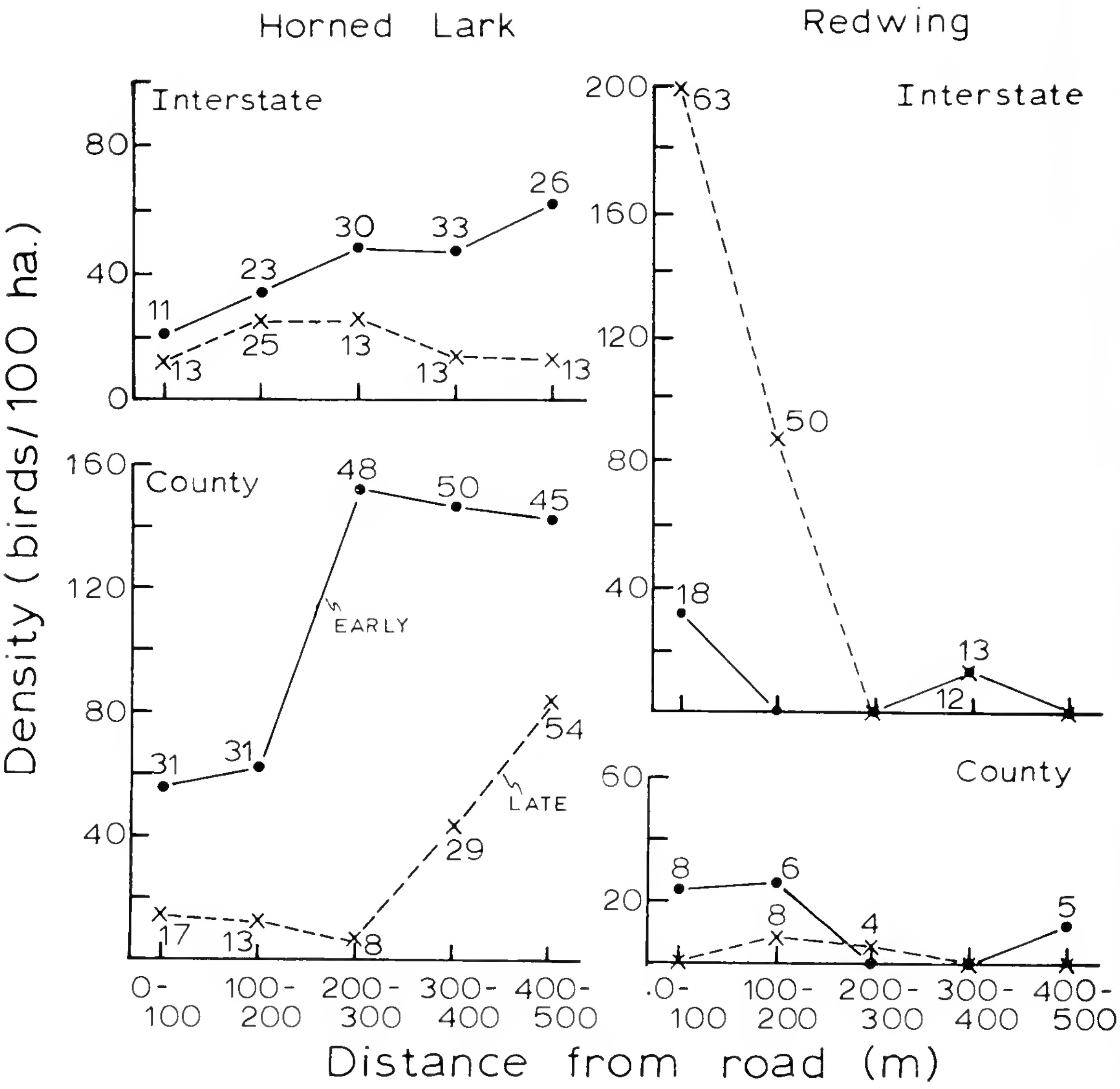

FIG. 1. Mean densities of Horned Lark and Red-winged Blackbird at varying distances from interstate and county highways in Illinois. Numbers indicate proportion of censuses that contained the species. Early censuses—10 Feb. to 11 Apr.; Late censuses—25 May to 20 June.

yield data sufficient for discussion here. Horned Larks, permanent residents in east-central Illinois, were observed throughout the study period. Migrating red-wings first arrived on 25 February.

Horned Lark densities increased with distance from the road for both county and interstate highways during the early census period and along county roads during the late census period; densities were generally higher along county than along interstate highways (Fig. 1).

Red-wing densities during the early census periods were generally low, with most birds observed near highways. During the late census period red-wings were very abundant in plots adjacent to interstate highways but rare or absent from distant interstate plots and throughout county road transects. The proportion of plots occupied by each species also varied considerably with road type and distance from the road (Fig. 1). (Two large, migrating flocks of red-wings found in the 400–500 m distance range were not included in Fig. 1.) The increased abundance of red-wings near interstate highways was associated with the wide right-of-way which included 10–15 m of bluegrass (*Poa pratensis*), often with shrubs or small trees.

In central Illinois, as in much of the midwest, most privately owned land is intensely cultivated. Nesting success of red-wings is partially determined by the availability of sturdy nest support sites early in the year (Orians, Ecol. Monogr. 31:285–312, 1961; Goddard and Board, Wilson Bull. 79:283–289, 1967), and although row crops probably are excellent feeding grounds for blackbirds, they certainly do not provide suitable nest supports until late in the year. The existence of right-of-way zones with extensive grass habitat and scattered shrubs should enhance nesting success and increase population density of red-wings. Water did not seem to be a factor, as our roadside transects did not include areas of water, even adjacent to interstates. Observed variation in density is consistent with this expectation. Uncultivated land adjacent to county roads is often no more than 2–3 m wide and is less likely to provide suitable nest supports, and populations of red-wings along county roads were much lower than along interstate highways.

The Horned Lark nests on bare ground, and cultivation of land formerly heavily vegetated has allowed this species to increase in numbers (Graber and Graber, Bull. Ill. Nat. Hist. Surv. 28(3):477–478, 504, 1963). Horned Larks seem to be most common in large expanses of open ground well away from other habitat types. This may account for low densities of Horned Larks in plots adjacent to highways. Alternatively, highway noise may affect them, perhaps by interfering with vocal communications. Our data do not allow testing of these hypotheses.

Data presented here demonstrate that highways affect abundance of bird species and that the effect varies with species, highway type, season, and distance from the highway. Future construction programs for highways should consider effects on wildlife, both in the immediate highway right-of-way and in areas at least up to 500 m from the right-of-way.

This research was a segment of Project #14–16–0008–1219 from the U.S. Fish and Wildlife Service to the Urban Wildlife Research Center. Funds for this project were provided by the Federal Highway Administration.—W. DWIGHT CLARK (DECEASED) AND JAMES R. KARR, *Dept. of Ecology, Ethology and Evolution, Univ. of Illinois, Champaign, IL 61820. Accepted 15 Dec. 1977.*

Wilson Bull., 91(1), 1979, pp. 145–148

Observations on Plush-capped Finches in the Andes with a description of the juvenal and immature plumages.—The Plush-capped Finch (*Catamblyrhynchus diadema*) remains today poorly known and of uncertain taxonomic status despite a relatively wide geographical range in the Andean highlands from Venezuela to Bolivia. The only published statements known to us regarding the behavior of this species are in Van Tyne and Berger (Fundamentals of Ornithology, John Wiley and Sons, 1976) from Jelski (*in* Taczanowski, Ornithologie du Pérou, Rennes, France, 3:25, 1886): "They are met with in isolated pairs or mingled with flocks of other birds," and Goodfellow (Ibis, 8th series, 1:473, 1901): "We found them [3 ♂♂] singly in the higher trees," and a brief account by Schafer and Phelps (Boletín de la Soc. Venez. de

Cienc. Nat. 84:158, 1954). Mention of Plush-capped Finches in more recent works largely recounts statements made by the above authors. In view of the lack of information about this species and its current position in a monotypic family, the following observations by Hilty in Venezuela and Colombia (1972–1977), Silliman in Colombia (1971–1972), and Parker in Perú (1974–1977) are of interest. The observations reported here were incidental to other work and our total observation time varied from less than 1 min to more than 15 min each time we observed Plush-capped Finches. Each of us has encountered Plush-capped Finches many times during our work in the Andes.

We found Plush-capped Finches in Colombia from 2600 m in humid subtropical forest with bamboo (*Chusquea* spp.) in the Western Andes on Cerro Munchique, Dept. of Cauca, to 3300 m at treeline in the Central Andes in Parque Nacional de Puracé, Dept. of Cauca. In the Santa Marta Mountains T. B. Johnson (pers. comm.) found them at 2200 m and 2775 m on the Cuchillo de San Lorenzo. In Perú the species is common in the bamboo (*Chusquea* sp.) understory of humid temperate forest from 2400 m to treeline at 2900–3050 m on the west slope of the Western Cordillera in the Dept. of Pirua above Canchaque, in the Carpish Mountains in the Dept. of Huánuco, and in the Dept. of Cuzco above the Urubamba drainage. In Venezuela Plush-capped Finches may occur somewhat lower in the coastal range where they have been observed at 1700–1800 m in Parque Nacional El Avila, outside Caracas (C. Parrish, pers. comm.) and at 1900–2000 m 30 km west of Caracas.

At all the above locations Plush-capped Finches appear to be resident in humid or brushy edge habitats where the bamboo (*Chusquea* spp.) grows. Their fondness for bamboo was noted by Schafer and Phelps (op. cit.). They appear to be bamboo specialists but are not wholly restricted to bamboo when foraging. We have also observed them foraging in tall grass, shrubby edges along roadsides, and once on bare ground at the edge of a road in Colombia (Hilty). Generally bamboo provides the preferred foraging site and the species is rarely far from it.

Plush-capped Finches forage on bamboo stalks by clinging upright, vertically, or upside down, adopting these chickadee (*Parus*)-like postures with versatility. They press their short swollen bill directly into the axiles of dense leaf whorls at each node. sometimes tugging vigorously, or running the bill along the bamboo stems with a series of tiny biting motions. With a short hop or sidling motion they progress quickly along a bamboo stalk out to the arching tips. Bamboo foliage, ferns, and other temperate vegetation are also searched by fluttering and flitting in restless fashion during which they apparently take small insect prey from leaf surfaces.

Silliman found that the stomach of a bird collected in Parque Nacional de Puracé, Colombia (G. Hubbard, No. 82, INDERENA, Popayán) contained small bits of bamboo leaf. A bird from the Dept. of Huánaco (D. Tallman, LSU 74752) also contained "vegetable matter" in the stomach and a bird taken at the San Lorenzo Experimental Station, Santa Marta (S. M. Russell and T. B. Johnson, UA 11161) had insect remains in the stomach.

Two points regarding the foraging technique are worth mentioning. First, the habit of probing into a tight clump of stems, leaves, or tight rosette of leaves is sometimes employed by other highland species, e.g., Streaked Tuftedcheek (*Pseudocolaptes boissonneautii*), which specializes in foraging at bromeliads, and Blue-backed Conebills (*Conirostrum sitticolor*), which may combine probing and gleaning movements in dense temperate shrubbery. These species and others are often flock associates of Plush-capped Finches but none appear to be bamboo specialists. The small tightly compressed leaves of many temperate zone shrubs in the tropics seem to encourage the use of probing motions when foraging, a technique less often employed by lowland birds that encounter larger leaves and less dense foliage.

Second, we speculate that the short, dense and plush-like (hence common name) feathers of the forecrown are less susceptile to feather wear than lax crown plumage. This may be adaptive for a species specializing in pressing its head into tight, partially woody and sometimes prickly leaf whorls of bamboo. Additionally, the plushy feathers might be effective in resisting soaking moisture from the dense leaf whorls that are almost constantly dripping wet from rain and fog at these elevations.

In contrast to Goodfellow (op. cit.), we found Plush-capped Finches foraging principally between 1 and 4 m above ground and less frequently from ground to 6 m. Usually in pairs, they are rarely seen away from mixed feeding flocks (1 time in 22 observations in Venezuela and Colombia by Hilty; very rarely in Perú). This may reflect both the tenacity with which so many temperate Andean species faithfully remain with mixed parties and their inconspicuousness when alone.

Foraging Plush-capped Finches utter soft high-pitched chipping notes not unlike those of the numerous finches and tanagers which they follow as flock associates. In Perú songs consisted of a monotone of not very musical chipping and twittering notes uttered in a series and lasting 15 sec to nearly 1 min. In quality and arrangement such songs are reminiscent of those of several *Hemispingus* tanagers. Common flocking associates of Plush-capped Finches in the Andes include: Agile Tit-tyrant (*Uromyias agilis*) in Colombia; Unstreaked Tit-tyrant (*U. agraphia*) in Perú; a wren (*Cinnycerthia*), Golden-fronted Redstart (*Myioborus ornatus*) in Colombia, Yellow-crowned Redstart (*M. flavivertex*) in Colombia's Santa Marta Mountains; Spectacled Redstart (*M. melanocephalus*) in Perú; Citrine Warbler (*Basileuterus luteoviridis*), Blue-backed Conebill (*Conirostrum sitticolor*), Golden-crowned Tanager (*Iridosornis rufivertex*) in Colombia; Yellow-scarfed Tanager (*I. reinhardti*) in Perú; Lacrimose Mountain-Tanager (*Anisognathus lacrymosus*), Black-capped Hemispingus (*Hemispingus atropileus*), Oleaginous Hemispingus (*H. frontalis*), and Gray-capped Hemispingus (*H. reyi*) in Venezuela; and several brush-finches (*Atlapetes* spp.).

The nesting biology of Plush-capped Finches has not been described but a juvenile was noted accompanying and being fed by 2 adults about 30 km west of Caracas, Venezuela, on 21 December 1976. Schafer and Phelps (op. cit.) mention May as the breeding season in Rancho Grande 40 km westward. For 15 Plush-capped Finches (*C. d. citrinifrons*) $\bar{x} = 14.3 \pm 1.7$ g.

Because the juvenal and immature plumages of Plush-capped Finches have not been described we present the following description from a series of specimens in the LSU Museum of Zoology (colors follow Ridgway, Color Standards and Color Nomenclature, Washington D.C., 1912). Immature: upperparts brownish-olive, including crown, nape, mantle, back, and rump, wings dusky narrowly edged brownish-olive, tail dusky and broadly edged brownish-olive, underside of tail brownish-olive, paler than adults, underparts light brownish-olive heavily washed with ochraceous-tawny. Some immature specimens approaching adult plumage show varying amounts of yellow on basal portion of feathers of forehead and forecrown and flecks of chestnut or orange-rufous on underparts. Iris brown to dark brown, legs gray-brown to blue-gray, bill brown to pinkish-gray (soft part colors from specimen labels). Juvenal: like immature but forehead gray and underparts plain brownish-olive with no ochraceous-tawny wash.

We thank Chris Parrish and Terry B. Johnson for useful information about Plush-capped Finches. George H. Lowery Jr., Louisiana State Univ. Museum of Zoology; Stephen M. Russell, Univ. of Arizona; and Richard C. Banks, U.S. National Museum, kindly allowed us to examine specimens in their care. John P. O'Neill and Lester L. Short reviewed the manuscript and suggested several useful improvements. Support and travel during these observations came from a Univ. of Arizona-Peace Corps Graduate Research Program and Bird Bonanzas Inc., (Hilty), the LSU Museum of Zoology (Parker), and the Peace Corps (Silliman).—Steven L. Hilty, *Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721;* Theodore A. Parker III, *Museum of Zoology, Louisiana State Univ., Baton Rouge, LA 70893; and* James Silliman, *Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721.* *Accepted 8 Dec. 1977.*

Wilson Bull., 91(1), 1979, p. 148

An observation of stick presentation by the Swallow-tailed Kite.—On 26 January 1977, while conducting field research in Saül, French Guiana, we observed a Swallow-tailed Kite (*Elanoides forficatus*) circling over the forest holding a long, narrow stick in its bill. The flight was maintained for several minutes, whereupon the individual, bird *A*, landed about 2 m from another kite, bird *B*, at the top of a 30 m dead tree. Keeping its head lowered, body flattened, and wings extended, *A* approached *B* along a horizontal branch. This was followed by both up and down and side to side movements of *A* during presentation of the stick to *B*. After about 30 sec posturing, *A* dropped the stick and flew off. The other bird remained impassive throughout the performance; preening after *A* had left. We observed *Elanoides* carrying sticks in their bills and noted chases and agonistic encounters numerous times in the ensuing weeks. Instances of males feeding females have been documented for the Swallow-tailed Kite during both nest-building and incubation (Snyder, Living Bird 13:73–97, 1974). In such instances, the male usually approached the perched female.

A nesting date in mid-March has been given for Swallow-tailed Kites in Surinam (Haverschmidt, The Birds of Surinam, Oliver and Boyd, Edinburgh, 1968). As kites in Saül were still in flocks of up to 10 individuals in late January, we interpreted our observations as ritualized nest-building, serving in the formation rather than intensification of the pair bond.

Our work in French Guiana was supported by the Watkins and Saül funds of the University of Kansas. We are grateful to R. F. Johnston, R. M. Mengel, E. C. Murphy, and J. T. Paul, Jr. for comments on the manuscript.—W. Bruce McGillivray, *Museum of Natural History and Dept. of Systematics and Ecology, Univ. of Kansas, Lawrence, KS 66045, and* David J. Brooks, *Dept. of Zoology, Univ. of Toronto, Toronto, Ontario, Canada M5S 2E1.* *Accepted 20 Dec. 1977.*

Wilson Bull., 91(1), 1979, pp. 148–149

Record of Puerto Rican Screech Owl, Turkey Vulture and Osprey from St. Croix, U.S. Virgin Islands.—The continued existence of the Puerto Rican Screech Owl (*Otus nudipes*) on St. Croix has been in question for some time although there have been reports of its calls (Leck, Condor 77:107, 1975). While attempting to capture deer at night on 21 January 1971 I observed a Puerto Rican Screech Owl on the ground in open pasture. It allowed approach within 10 m and was illuminated by a 100,000 candlepower spotlight while being observed through 7 × 50 binoculars. It flew to a fence post and was again approached with a spotlight before departing to dense forest. On 14 November 1972 I found a Screech Owl standing on a road; it allowed close approach while being illuminated by the headlights. Both sightings were in a sparsely inhabited area northeast of Frederiksted.

In July 1972 I observed a Turkey Vulture (*Cathartes aura*) feeding on a dead mongoose (*Herpestes auropunctatus*) on a rural road near Annaly Bay. I made 2 additional sightings on 21 and 22 April 1975 of a Turkey Vulture soaring above Davis Bay. Both sightings were from a steep hill overlooking the bay which allowed close views of the vulture.

Ospreys (*Pandion haliaetus*) have not been recorded nesting on St. Croix, but Leck (op. cit.) records a summer pair. In May 1974 I saw a pair of Ospreys building a nest in a mahogany tree (*Swietenia* sp.) at the top of a hill near the sea west of Christiansted. I heard much calling at 2 other sites within 0.5 km but did not confirm additional nests or pairs.—David W. Nellis, *Virgin Islands Dept. Conservation and Cultural Affairs, St. Thomas, U.S. Virgin Is. 00801. Accepted 30 Jan. 1978.*

Wilson Bull., 91(1), 1979, pp. 149–150

Chestnut-colored Woodpeckers feeding as a pair on ants.—The Chestnut-colored Woodpecker (*Celeus castaneus*), which Slud (Bull. Am. Mus. Nat. Hist. 128:1–430, 1964) describes as a "seldom-seen" bird, is difficult to follow for any length of time in Caribbean lowlands of Central America. When I succeeded in watching 1 individual for 30 min on 9 January 1977 at Tikal, Peten, Guatemala, it made rapid glancing blows on a branch, nearly all of them too weak to be audible. The woodpecker seemed to find much to feed on in some places, and I noticed that all of the trees that it worked on had termite tunnels running up them. The same was true on other days when I had briefer views. At no time did I have a clear view of what the woodpecker was feeding on nor have I been able to find any accounts in the literature.

On 7 January I noticed 2 of these woodpeckers feeding on a palm tree 8 m above the ground. One bird pecked at the dry, loose dead bracts at the base of an arching stem from which hung a large flower. As it pulled fluffy material from among the bracts, small black ants, more than it could consume with rapid feeding motions of bill and tongue, ran or fell down onto the flower cluster. Here they were picked up by the second Chestnut-colored Woodpecker perched 30 cm below the 1st one. The ants were clearly seen with an 8 × 40 field glass and I watched for 15 min.

An interesting feature of the feeding was the way 1 woodpecker took advantage of the other's pecking and disturbing the ants in the bracts above, the 2 being thus enabled to feed together. Feeding as a pair has been noted for *C. brachyurus*, an Asian species, by Short (Bull. Am. Mus. Nat. Hist. 152: 292, 1973).

Although he gives no accounts of feeding habits, Wetmore (Smithson. Misc. Coll. 150(2):541, 1968) states of *C. castaneus* that "The salivary glands—were large, extending the full length of the mandibular rami. As I skinned the heads the mucous secretion adhered like a gum to my fingers." Secretions of this type would seem to place *C. castaneus* in a group with other ant-eating species such as the Common Flicker (*Colaptes auratus*) and the European Green Woodpecker (*Picus viridis*) that have large salivary glands providing an insect-holding or formic acid-neutralizing film (Welty, The Life of Birds, Saunders, New York, 1962).

There are areas of lower trees and thicker vegetation in the forest at Tikal and it was in one of these that I observed the Chestnut-colored Woodpecker. The species is sexually dimorphic. In poor light, however, I could not be sure whether the birds observed were male and female, even though both appeared to be adults. I thank Lester L. Short for reading and commenting on this note.—LAWRENCE KILHAM, *Dept. of Microbiology, Dartmouth Medical School, Hanover, NH 03755. Accepted 20 Dec. 1977.*

Wilson Bull., 91(1), 1979, pp. 150–151

Off-lek copulation in Sharp-tailed Grouse.—The Sharp-tailed Grouse (*Pedioecetes phasianellus*) is a lek species (Hjorth, Viltrevy 7:184–596, 1970). While males typically gather in morning and evening at specific sites to establish territories and display, some have been reported displaying as solitary birds (Hammerstrom, Wilson Bull. 51:105–120, 1939; Amman, Michigan Dept. Cons. Rept., 1957). There has previously been no evidence that lone males copulate successfully with females at these sites. I observed a copulation at such a site at 19:52 on 2 June 1976.

A solitary male Sharp-tailed Grouse was seen displaying on a trail 5 km south of Chatfield, Manitoba (50° 47′ N, 97° 34′ W). A female grouse walked onto the trail 3 min later and the male intensified his display. The second grouse remained at the trail edge for 12 min before walking to the center where it crouched in a precopulatory position. The male mounted this bird and after copulating successfully continued to display. The female ruffled her feathers, preened, and walked off the trail 4 min after copulation. The male continued displaying until I flushed it 22 min later. I checked the next morning and saw 1 non-displaying Sharp-tailed Grouse within 50 m of the above site. On subsequent checks no grouse were observed at this location.

From studies of grouse since 1969 in the Chatfield area (McKay and Carmichael, Manitoba Dept. Mines and Nat. Res. MS Rept., 1970) I was familiar with the locations of known past and present leks. The site described above was not an established lek and had not been used before or during 1976 or 1977. Two nearby leks (500 m and 800 m), with 16 and 22 males, were active (audible from site) when the observed copulation occurred.

Hamerstrom (Ph.D. Thesis, Univ. of Wisconsin, 1941) and Petcrle (Ph.D. Thesis, Univ. of Michigan, 1957) observed solitary males "daneing" and attracting females but saw no copulation at these sites. Others have suggested that mating does sometimes occur off the lek (Lehmann, North Am. Fauna 57, 1941; Symington and Harper, Saskatchewan Dept. Nat. Res. Cons. Bull. No. 4, 1957). Hjorth (op. cit.) reported "solo" displaying male Black Grouse (*Lyrurus tetrix*) and concluded many, if not most, copulations occur away from leks. Kruijt et al. (Proc. XV Int. Ornithol. Congr. 399–423, 1970) studied male Black Grouse that displayed solitarily at fixed sites and found these males often copulated successfully. My observation provides evidenee that similar behavior occurs in North American lekking grouse.

Rippin and Boag (J. Wildl. Manage. 38:616–621, 1974) found nonterritorial males in a population of Sharp-tailed Grouse and suggested that sinee they did not attend a lek they were a nonreproductive element in the population. Robel (J. Wildl. Manage. 34:306–312, 1970) found a similar situation with Greater Prairie Chicken (*Tympanuchus* *cupido*). Such males may represent a segment of the population that display solitarily. Robel (op. cit.) noted that female aggressive behavior at leks may prevent mating of subordinate females. It is possible that non-lekking males and subordinate females contribute to the reproducing output of the population by mating off the lek. The incidence of such mating may be dependent on population and aggression levels as suggested by Robel (Proc. XV Int. Ornithol. Congr. 121–133, 1970).

These observations were made while I was engaged in studies of movements and habitat use of female Sharp-tailed Grouse. Financial support was provided by the Manitoba Department of Renewable Resources and Transportation Services. I thank S. G. Sealy and R. Wishart for constructive comments.—DONALD A. SEXTON, *Dept. of Zoology, Univ. of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2.* *Accepted 10 Apr. 1978.*

Wilson Bull., 91(1), 1979, pp. 151–154

Differences between nestlings and fledglings of Screaming and Bay-winged cowbirds.—Authors that have written about brood parasitism of Screaming Cowbirds (*Molothrus rufoaxillaris*) on Bay-winged Cowbirds (*M. badius*) have stated that the nestlings of both species are so similar in appearance, behavior, and vocalizations that they cannot be told apart. They also state that the resemblance of the 2 species persists through the post-fledgling period until the young Screaming Cowbird begin molting into the black adult plumage (Hudson, Birds of La Plata. Vol. 1, J. M. Dent and Sons, Ltd., London, 1920:105; Friedmann, The Cowbirds, C. C. Thomas, Springfield, Ill., 1929:52, 54; see also summary in Lack, Ecological Adaptations for Breeding in Birds. Methuen, London, 1968:94). Without denying the high degree of similarity between the juveniles of both species I will describe the differences that can be observed between the young of the host and the parasite.

All data reported here were collected near Lobos, Buenos Aires Province, Argentina. I have published a short preliminary account on both species (Fraga, Auk 89:447–449, 1972).

At hatching both species have a reddish skin color, but as soon as their skin has dried it can be noted that the skin of nestling bay-wings is orange. The bill is pinkish with a darker pigmented area around the white eggtooth. There is some variation in the size, shape, and color of this pigmented area but the subterminal dark tip of the bill is usually conspicuous upon close examination.

Nestling Screaming Cowbirds have pink or pale pink skins. The bill is also pinkish, but it lacks a dark pigmented area around the white eggtooth (Fig. 1).

I discovered these differences in the breeding season of 1971–1972. Since that time I have followed the development of 57 young birds that initially had orange skin and dark bill tips. These 57 juveniles, which I banded, survived at least 2 months after leaving the nest; 36 of these lived 1 year or more. All of these turned out to be bay-wings. Up to 1977 I also followed the development of 11 banded nestlings with pink skins and uniformly colored bills, and that survived for at least 45 days after leaving the nest; all of these turned out to be Screaming Cowbirds. The same differences were also detected in an additional sample of 31 nestlings of both species hatched from marked and measured eggs found in bay-wing nests. As a rule they confirmed my prior identification of the eggs. I do not know if the above mentioned differences in the coloration of the nestlings occur over the entire range of the species.

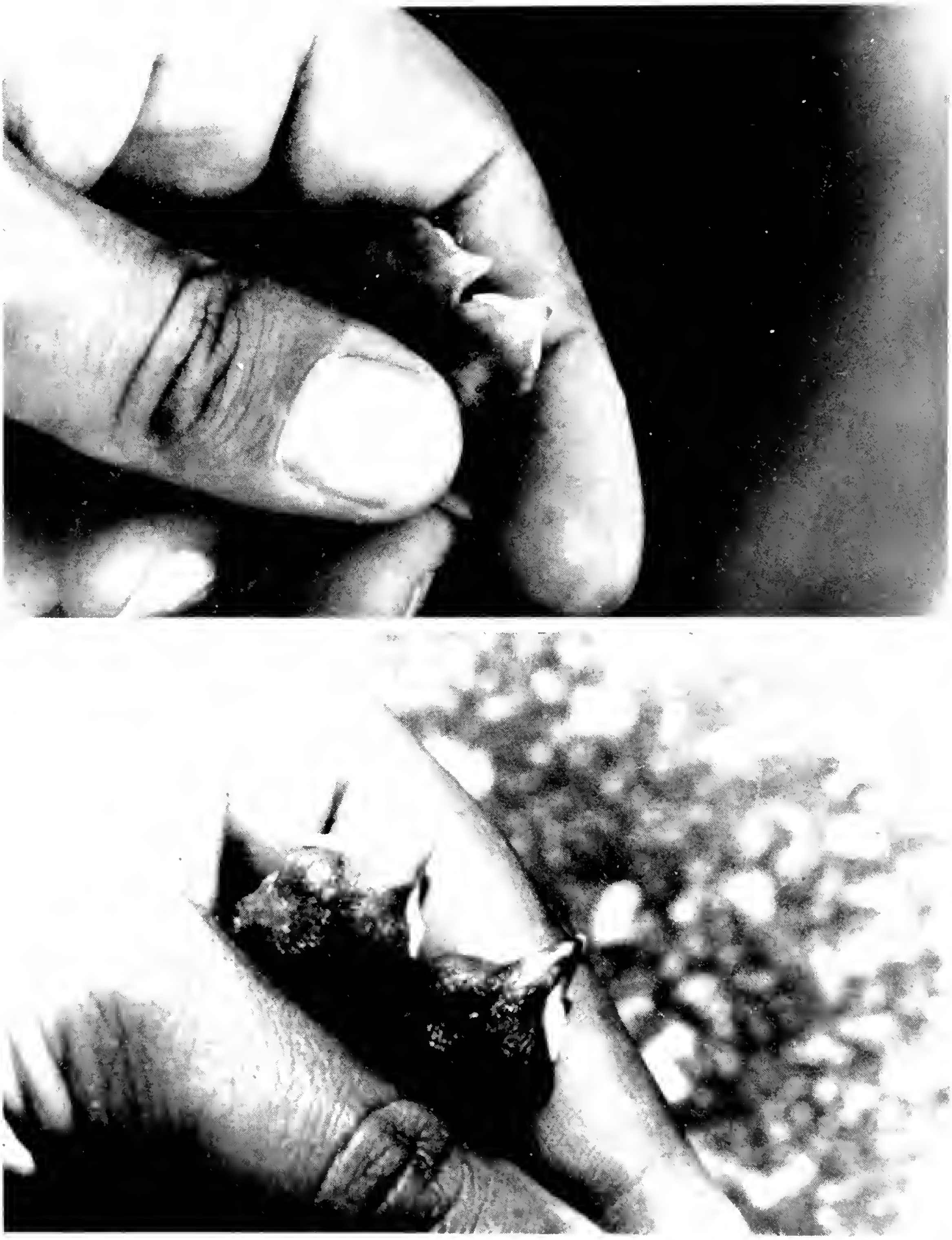

FIG. 1. A) Above, recently hatched nestling Screaming Cowbird with a uniformly colored bill. Below nestling bay-wing showing the dark pigmented area around the eggtooth. B) The same nestlings on day 4: the difference in bill coloration is conspicuous.

The difference in the hue of the skin does not usually persist through the whole nestling period and after day 4–5 I could no longer distinguish between nestlings of the 2 species. There is a possible difference in bill color between the 2 forms. Bills of older Screaming Cowbird nestlings seem paler than those of nestling bay-wings.

FIG. 2. Nestling Screaming Cowbird (right) with 3 bay-wing nestmates. The hatching interval between the parasitic nestling and the 2 following host nestlings was less than 7 h.

but this difference was noticed only in a sample of 11 nestlings. During the post-fledgling period the bills of young Screaming Cowbirds darken to black whereas young bay-wings retained dark brownish bills with lighter tips (cf. Friedmann, op. cit.:31–32) which slowly darkened to black in 2–3 months.

Of interest would be more information on the color of the nestlings of other species of icterids. For comparative purposes I will mention that nestling Shiny Cowbirds (*Molothrus bonariensis*) in my study area have basically orange skins, but they resemble nestling Screaming Cowbirds in having rather uniformly colored bills, in either the white or yellow flanged form (for further details on the appearance of Shiny Cowbird nestlings see Fraga, Wilson Bull. in press).

Differences in weight.—Differences in weight between nestling Bay-winged and Screaming cowbirds of the same or similar age depend on variables such as the order of hatching, the brood size and the number of attendant adult bay-wings. In favorable circumstances the parasitic nestlings outweigh their nestmates, but starving nestlings may belong to either species. In some nests the difference in size and weight was outstanding (Fig. 2).

Hudson (op. cit.:105) correctly pointed out a slight difference in size between fledgling Screaming Cowbirds and bay-wings. Sometimes this difference is really conspicuous in the field, as some fledgling Screaming Cowbirds visibly surpass in size the adult bay-wing attendants. Adult bay-wings in my study area weighed 39–51 g (N = 24; $\bar{x}$ and SE: 44.48 g ± 0.65, data up to 1976). The weights of 3 extremely large Screaming Cowbird fledglings were 59, 58, and 54 g.

Lowther (Wilson Bull. 87:481–495, 1975) among others, states that Screaming Cowbirds are sexually monomorphic in size. Hudson (op. cit.: 96) correctly recorded a size difference between the sexes, which seems to occur at least in Buenos Aires Province, Argentina. In my study area Screaming Cowbirds are sexually dimorphic in size (weights of 4 males: 66, 64, 62 and 61 g; 5 females: 52, 51, 51, 49 and 48 g). Quite probably the overly large nestling and fledgling Screaming Cowbirds were males.

Differences in behavior and vocalizations.—There are several differences in behavior and vocalizations between Screaming Cowbirds and bay-wings, and some of these may be detected among the juveniles of both species. For instance, adult bay-wings practice allopreening, and fledgling bay-wings often beg preening by assuming the Allopreening Invitation Posture (described in Selander, Auk 81:394–402, 1964). I have not seen this posture among young or adult Screaming Cowbirds. Young Screaming Cowbirds may start to utter their unmistakable adult vocalizations in subdued versions when still in the juvenal, bay-wing-like plumage.—ROSENDO M. FRAGA, *Guido 1698, 16B, 1016, Buenos Aires, Argentina.* *Accepted 1 Mar. 1978.*

Wilson Bull., 91(1), 1979, p. 154

Chimney Swift nest found in hollow tree.—On 3 August 1977 K. D. Blodgett discovered a Chimney Swift (*Chaetura pelagica*) nest in a live, hollow silver maple (*Acer saccharinum*) when he removed the tree to free power lines.

The most recent record we found of a Chimney Swift nesting in a tree was that reported by Hofslund in 1958 (Wilson Bull. 70:192) and fewer than 10 others have appeared in the last 100 years. The nest tree described here was in a quiet residential area in Kinderhook, Illinois, a small rural community on the eastern bluff overlooking a floodplain of the Mississippi River. There were 3 or 4 large silver maples and several smaller ornamental trees on the 0.2 ha lawn in the nest-site area. The crown of the nest tree was continuous on 1 side with that of another silver maple of similar size. The nest tree was about 1 m in diameter at the base, 70 cm diameter at the nest level, and 25 m tall. The inside of the tree cavity was about 50 cm in diameter at the nest level. While the tree was being cut, Blodgett saw a Chimney Swift ascend from a 25 cm opening in a broken stub that extended about 10 cm from the trunk at about 4 m above the ground—well below the canopy. The bird circled the tree about 1 min, flying within 4 m of the workmen using a chain saw. The bird's behavior and the excellent condition of the nest indicated that the nest was probably used in 1977. It was glued to the SE wall of the tree cavity about 3 m from the ground. It was identified by Edwin C. Franks and R. M. Zammuto and is preserved in the biological collections of Western Illinois University.—K. DOUGLAS BLODGETT AND RICHARD M. ZAMMUTO, *Dept. of Biological Sciences, Western Ill. Univ., Macomb, IL 61455.* *Accepted 10 Apr. 1978.*

Wilson Bull., 91(1), 1979, pp. 154–155

Notes on the reproductive behavior of the Yellow-billed Cuckoo.—On 20 May 1964, my Ornithology class and I were in open bottomland second growth forest along the Allegheny River near Allegany, Cattaraugus Co., New York, and observed a precopulatory display by a Yellow-billed Cuckoo (*Coccyzus americanus*). The bird was in a position that has been described by Hamilton and Hamilton (Proc. Calif. Acad.

Sci. 32:405–432, 1965) as an intention movement to flee, with tarsi horizontal to the limb, and head and tail elevated. The bird then lowered its tail so that it pointed towards the ground, then raised it 180 degrees to point straight up. This movement was repeated 6 to 8 times after which another bird that we assumed was a male flew in and copulated—depressing his tail and moving it laterally towards the exposed cloaca of the female. He continued copulating about 5 sec and flew off. About 2 min later, the presumed female, resumed the precopulatory display, pumping the tail as described above. The male immediately flew down and a second copulation occurred.

On 11 June 1976, in company with Richard J. Clark, we observed a Yellow-billed Cuckoo breaking off small twigs in Cain Hollow of Quaker Run, Allegany State Park, in southwestern New York. After a few minutes it flew to a nest upon which another cuckoo was sitting and presented the twigs to the sitting bird which then placed them in the nest. Between 09:00 and 09:30 we observed this cuckoo bring 2 sticks, each about 15 cm long, and 4 beaksfull of what appeared to be pine needles and grass and present them to the sitting bird, which then tucked the material into the nest. Finally the cuckoo sidled up to the sitting bird and exchanged positions with it on the nest. No vocalizations were heard during the period of our observations. The next day Clark checked the nest and found 2 eggs. We presumed that the female was still in the process of laying because 3 to 4 eggs are a normal clutch at this latitude. Two weeks later he checked the nest again and found it empty. The nest was located 2.4 m from the ground on a 5 cm diameter horizontal branch and about 2.4 m out from the trunk of a pignut hickory (*Carya glabra*). The site was near the edge of a mature wooded area where second growth was invading an abandoned pasture.

These observations add to our knowledge of the Yellow-billed Cuckoo as no previous description of this distinctive precopulatory display has been published. Hamilton and Hamilton (op. cit.) described 1 attempted copulation in the western subspecies (*C. a. occidentalis*) which was similar to our observation except it lacked the tail pumping.

The bringing of nest material at the time of, and then following, the laying of the eggs is reminiscent of accipitrid and Purple Martin (*Progne subis*) behavior where green vegetation is brought to the nest. Stick offering is a common pair bond behavior in the Roadrunner (*Geococcyx californianus*) as is a vertical tail flick in the female, preceding a successful mount by the male (Whitson, The Living Bird, 14:215–255, 1975).

I suggest that the presentation of nesting material to a sitting bird aids in strengthening the pair bond in the same manner as courtship feeding and dueting function in other species (Skutch, Parent Birds and Their Young. Univ. Texas Press, 1976:18–20). Stephen W. Eaton, *Dept. of Biology, St. Bonaventure Univ., St. Bonaventure, NY 14778.* *Accepted 14 Apr. 1978.*

ORNITHOLOGICAL NEWS

1979 ANNUAL MEETING

The 60th annual meeting of the Wilson Ornithological Society will be held in Omaha, Nebraska, April 5–8, 1979. The meeting will be hosted by The Nebraska Ornithologists' Union and the Department of Biology, University of Nebraska at Omaha.

A special feature of the meeting will be a symposium on the biology of bird species with restricted ranges, organized by Drs. Jon Barlow and Toby Gaunt. Field trips are planned to include waterfowl concentrations on the Missouri River, Sandhill Cranes on the Platte River, and a visit to a prairie chicken lek. The chairman of the Local Committee is Dr. Roger S. Sharpe, Department of Biology, University of Nebraska at Omaha, Omaha, Nebraska 68182.

FIRST IBERO-AMERICAN MEETING ON ORNITHOLOGY AND WORLD MEETING ON ECOLOGY AND BIRD BEHAVIOR

This Meeting will take place in the city of Buenos Aires, Argentina, during the last week of November 1979 (11/25–12/1) under the sponsorship of the Asociación Ornitólogica del Plata and the collaboration of various local and international Institutes, Schools and Research Centers.

Work sessions and lectures will be held, concerning: (1) anatomy, physiology and genetics; (2) paleontology, phylogeny, taxonomy and zoogeography; (3) ecology and migrations; (4) ethology; (5) protection and conservation; (6) applied ornithology; (7) methodology for ornithological investigation, management and education; and (8) history, bibliography and miscellaneous.

The official languages of the Meeting will be Spanish, Portuguese and English. Presentation of papers and communications are welcome. Their abstracts should be received before March 31, 1979, containing fewer than 300 words. Registration fees vary from US $50.00 to US $200.00, according to kind of membership. Inscriptions, suggestions and requests for more detailed information should be sent to: Prof. Juan Daciuk, President, Organizing Commission, 1er. Encuentro Iberamericano de Ornitología, Casilla de Correo 3368, 1000 Buenos Aires, Argentina.

CALENDARS AVAILABLE

Arrangements have been made to publish and sell a "Fuertes Calendar" using one of the drawings each month. The first series will be available for 1979, and there are enough drawings to last over 20 years. The Arnold Printing Company, for years the printer for P. R. I., will print the calendars at cost. The net income from the sale of these calendars will be divided equally between the P. R. I. and the DeWitt Historical Society of Tompkins County, New York (another agency in which Katherine is interested, and which is taking the lead responsibility in publishing and selling the calendars). The calendars will cost $4.00 each (plus applicable sales taxes), or $4.50 postpaid. If everything goes as expected, we anticipate that for each calendar sold, the Katherine V. W. Palmer Fund will receive $1.00. Make checks payable to: DeWitt Historical Society, 118 N. Cayuga St., Ithaca, NY 14850.

Wilson Bull., 91(1), 1979, pp. 157–162

ORNITHOLOGICAL LITERATURE

NESTING ECOLOGY OF CANADA GEESE IN THE HUDSON BAY LOWLANDS OF ONTARIO: EVOLUTION AND POPULATION REGULATION. By D. G. Raveling and H. G. Lumsden. Ontario Ministry of Natural Resources, Fish and Wildlife Research Report No. 98, 1977: 77 pp., photographs, maps, graphs, paper cover. $3.50. (Available from Ontario Government Bookstore, 880 Bay St., Toronto, Canada M5S 1Z8.)—The main purposes of this report are "to present the results of investigations of apparent optimum and accomplished reproductive rates, habitat preferences, and density and spacing of nests in relation to the regulation of population size." This use of terminology is unfortunate as the report contains nothing about "population regulation." Rather, the emphasis is on factors limiting population size. The study is, in effect, the breeding and population biology of the Mississippi Valley Population (MVP) of Canada Geese (*Branta canadensis interior*). The geese nest in the Hudson Bay Lowlands and winter in southern Illinois, western Kentucky, southeastern Missouri and western Tennessee. The nesting study was done during 1967, 1968, and 1969 at Kinoje Lake (90 km west-northwest of Moosonee) and a surrounding area of 412 km^2. The MVP is one of the most important populations of Canada Geese in North America, both economically and in terms of its numbers. Before this report, very little was known of the subspecies' breeding habits and adaptations to the northern environment.

The report is presented in 2 sections: Nesting Ecology (Part I) and Population Limitations (Part II). Part I includes a 2 page description of snow conditions, precipitation, ice conditions, water levels and air temperatures on the study area. The remainder discusses the usual breeding biology topics such as arrival on the nesting grounds, egg-laying, nesting habitat, spacing of nests, clutch-sizes, nesting success, predation and general behavior. The authors report that as open water prevails at the nesting area, the geese disperse over the available habitat. Arrival in the north coincided with the average time of snow thaw and initial open water. Preferred nesting habitat consisted of small ponds (0.4–2 ha) containing 2 or more low, small islands that provided protection from predators throughout the nesting season. Nest success averaged 80%. Most nest losses were attributed to predators such as Ravens (*Corvus corax*), Herring Gulls (*Larus argentatus*), wolves (*Canis lupus*) or red foxes (*Vulpes fulva*).

The authors discuss at length their ideas on the evolution of clutch-size. This is the only section of the report that discusses evolution. They suggest that clutch-size may have evolved so that egg-laying ceases when the accumulated spring reserves are depleted to the point where the post-laying body weight approximates that of the winter body weight. The incubation period is thus described as a starvation regime. Unfortunately their hypothesis is based on the collection of only 4 late-nesting females. Certainly the authors erred in not considering recent work on the evolution of clutch-size in the Lesser Snow Goose (*Anser caerulescens caerulescens*), which, for the most part, counters their proposed scheme.

Part II is a compilation of data on winter distribution, population size, and mortality: the major objective "was to examine the nesting ecology of MVP Canada Geese to provide insight into the factors limiting their numbers." The size of the MVP, after most mortality from hunting, averaged 350,000 geese between 1966 and 1970 (from winter inventories in Wisconsin and Illinois). The authors conclude that "the population was clearly not limited on the summer range" and that "winter mortality was the major limiting factor for MVP geese and this mortality was overwhelmingly accounted for by hunting." These conclusions are not justified by their data. For example, in 1967 (a "retarded spring nesting season") they calculated that non-nesting and mortality of broods depressed the autumn population by 13% (37,000 geese) over that expected from an excellent nesting season; the calculated hunter kill that autumn/winter was 36,000 geese. More significantly, in 1968, "an excellent nesting season," 147,000 goslings (of 270,000 hatched) died before October; hunters killed 43,000 geese that autumn. Clearly, some limitation of population size occurs on the breeding grounds. The data suggest that mortality from hunting is largely density-independent, probably because the kill is controlled by a quota system. As the authors have little data on whether gosling mortality is caused by density-dependent or independent factors, they are unable to say what is regulating population size (wolf predation on nests was density-dependent). The authors concluded that the nesting grounds could support additional geese if the conditions recorded during this study prevail; unknown, however, is whether the additional breeding geese would have resulted in a net increase in gosling production. From a wildlife management viewpoint, hunting is certainly the mortality factor most easily manipulated. Thus the authors rightly suggest that the harvest in non-quota areas, such as the Kentucky side of the Ohio River, should be closely monitored.

This monograph contains numerous data: 54 tables, 34 figures, 2 appendices. There are 123 references, the latest of which is unfortunately 1974. The use of the word "predated," referring to what predators do to goose nests and eggs, is undefined in our dictionaries. Although we did not check all the statistics, there is an error in Table 39. The student's t value of 1.78 under "width of eggs" results in $P > 0.05$ instead of the reported $P < 0.05$.

For anyone interested in avian ecology, population biology and/or boreal ecology, this report is interesting and provides an opportunity for the serious investigator to compare the results with concurrent and later work, now in the literature, on other arctic and subarctic nesting geese.—JOHN P. RYDER and C. DAVISON ANKNEY.

THE BIRD WATCHER'S DIGEST. A new bimonthly magazine reprinting popular articles about birds from North American newspapers. Price: $1.50 per copy, or $7.50 per year in the U.S. and territories, $9.00 elsewhere. Pardson Corp., Box 110, Marietta, OH 45750.

BIRD BEHAVIOUR. This is a new journal of avian behavior and behavioral ecology. Two numbers have been published; the original name *The Babbler* having been changed with volume 1, number 2. The price is 75 cents (Australian) an issue. For further information write to J. J. Counsilman, Box 115, Indooroopilly, Queensland, Australia 4068.

IMPACTS OF TRANSMISSION LINES ON BIRDS IN FLIGHT. By Michael L. Avery (ed.). Biological Services Program, U.S. Fish and Wildlife Service, 1978: 151 pp., paper cover. Price not given. Document FWS/OBS-78/48. For sale by Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402.

AVIAN MORTALITY AT MAN-MADE STRUCTURES: AN ANNOTATED BIBLIOGRAPHY. By Michael L. Avery, Paul F. Springer, and Nancy S. Dailey. Biological Services Program, U.S. Fish and Wildlife Service, 1978:108 pp., paper cover. Price not given. Document FWS/OBS-78/58. Available as stock number 024-010-00472-0 from Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402.

SPECIES INDEX TO FLORIDA BIRD RECORDS IN AUDUBON FIELD NOTES AND AMERICAN BIRDS, VOLUMES 1–30, 1947–1976. By Margaret Coon Bowman. Special Publication No. 1, Florida Ornithological Society, 1978: 42 pp., paper cover. $3.75.—Available prepaid from the Treasurer, Florida Ornithological Society, 1701 NW 24th Street, Gainesville, FL 32605.

BIRDS OF THE SOUTHWEST PACIFIC. By Ernst Mayr. Charles E. Tuttle Co., Rutland, VT, 1978 (1945): 316 pp., 3 color plates, 16 line drawings, map. $5.75.—This is a reprint of the 1945 book. The first part deals with birds arranged by taxa, in 3 chapters covering seabirds, shorebirds, and land and freshwater birds. The second part contains 7 chapters reviewing the birds by geographical regions, specifically Samoa; Fiji, Tonga, and neighboring islands, New Caledonia and Loyalty Islands; the New Hebrides and Banks Islands; the Santa Cruz Islands; the Solomon Islands, and Micronesia.—R.J.R.

GUIDE TO THE IDENTIFICATION AND AGEING OF HOLARCTIC WADERS. By A. J. Prater, J. H. Marchant and J. Vuorinen. British Trust for Ornithology Field Guide No. 17, British Trust for Ornithology, Tring, Herts., England. 1977. 168 pp., 1 color plate (2 photos), 16 black and white plates (32 photos), 10 figures and numerous text illustrations. £2.50 or $6.00 (U.S.), including postage.—This book is a 'must' for all banders trapping shorebirds in North America and for anyone else who is interested in improving their ability to age shorebirds both in the hand and in the field. Very little useful information has been brought together previously on this topic and the present volume goes a long way towards filling the gap. Much of what has been previously available has either been scattered through the literature in papers or handbooks, often in a form not very suitable for field use, or has dealt with anatomical techniques (e.g., bursa of Fabricius, cranial pneumatisation) which are either inapplicable to live birds or of no value for shorebirds (R. McNeil and J. Burton, Wilson Bull. 84:329–339, 1972), or flight feather characters which appear to be unreliable (J. Burton and R. McNeil, Bird-Banding 47:201–209, 1976). The authors have drawn together information obtained from shorebird collections in various museums, as well as from extensive field observations made by banders throughout the world, to present a series of plumage and structural characters that may in many instances enable the age of the bird to be readily determined, and which may be of use in determining its sex or racial origin.

The book itself covers 117 species of shorebirds breeding in the Palaearctic and Nearctic faunal regions and is thus equally useful to European and North American workers. For each species, information is presented on distribution and migration, identification, ageing, sexing, geographical variation and biometrics. References on particular topics are listed with each species account and there is also a general bibliography. European terminology is used throughout the book, and there is a comparison of age codes and moult terminology used by workers in Europe and North America in the introduction for those not familiar with the equivalent terms. The book is quite well produced for field use, being bound in a water-resistant thin card cover, and measuring 15 × 21 cm. The 32 black-and-white photographs by J. B. and S. Bottomley are outstanding, and the book deserves special mention for the two magnificent, exclusive color photographs by Dr. V. Flint of a Spoon-billed Sandpiper and Lesser Sandplover on nests in northeastern USSR.

The book is clearly intended primarily for the use of banders who are able to examine shorebirds in the hand, though it will also be of interest to museum workers and taxonomists for its information on plumage and geographical variation. Much of the information can also be applied in the field and is thus of interest to bird watchers: the photographs are excellent in illustrating many of the ageing features referred to in the text.

The authors are generally aware of the present shortcomings of the book and point out that it is intended very much as a first edition, to which a great deal of further information can be added as it becomes available from the large amount of fieldwork presently being undertaken on shorebirds in Europe, North America and Africa. One area in which the book could do with expansion is on moult processes in 1-year-old birds wintering in tropical areas, where replacement of outer primaries or more complicated moult patterns may be of considerable use in ageing individuals (e.g., Stilt Sandpipers and Solitary Sandpipers in Surinam may moult outer primaries during their first winter (A. L. Spaans, pers. comm.)). Information on brood patches would also be useful. Hopefully, more extensive data on measurements of different races and species will become available, and it would be helpful to include field measurements of live birds as well as those of museum specimens. There are some inaccuracies which should also be weeded out. For instance, North American populations of the Red Knot do not generally suspend their primary moult during migration between North and South America, a misconception that appears to have arisen from the literature. Recent evidence indicates most of the population migrates to the wintering quarters in South America before moulting, though some may moult and perhaps subsequently remain to winter on the U.S. eastern seaboard.

In general, the book is to be highly recommended. For anyone banding shorebirds it is indispensable. I found the book useful and accurate in the field in 1978, and hope that other banders will use the book and contribute information towards the production of a more robust second edition.—R. I. GUY MORRISON.

BIRDS IN PERIL. By John P. S. Mackenzie, illustrated by Terence Shortt. Houghton Mifflin Co., Boston, 1977: 191 pp. $14.95.—This book is an account of the historical background, current status, and future prospects for existence of most species and subspecies of endangered North American birds. Although the author notes that 32 species or subspecies of continental North American birds are included on the Endangered Species List, such taxa as the Golden-cheeked Warbler, Red-cockaded Woodpecker, Yuma Clapper Rail, and so on, are not included within the 20 species selected for detailed treatment. Before the individual species accounts, which compose the bulk of this volume, there is a very brief section (overly brief, I would say) dealing with a smattering of bird evolution, bird life in North America before European man's arrival, examples of species which have "shuffled off the mortal coil" (the Dodo, Great Auk, Passenger Pigeon, Heath Hen), and some causes of extinction (DDT, hunting pressure, etc.). The species accounts generally include a short historical sketch of the endangered bird, various facts about the animal's life cycle, some observations on behavior, food habits, and habitat requirements, a discussion of the factors that led to the decline of the species, using population size estimates over the years to document the event, and a section on conservation efforts including the future prospects for avoiding extinction. The text is well written; the style is attractive; the information is accurate; and the illustrations transcend the scientifically accurate depiction of a species to convey the life of a species. They are truly artistic and superb.

I wish to go beyond a mere review of this enjoyable volume, however, to say a bit about books of this sort and extinction in general. Presumably the author wrote this book to inform people about the fact of extinction, its causes (particularly those correlated with human activity), and the efforts being expended to reverse the trend toward extinction of a few species. Many books are available on this subject; many bureaucrats are supported by endangered species; many species are going extinct and little is being done to save them. I wish to consider the following postulate: extinction is part and parcel of evolution; efforts at reversing human-related extinction are futile and likely to remain so; and books of this genre mislead people by implying that effective efforts are underway to reverse the environmentally unsound practices of humans around the world.

We know that extinction has been a part of life since life evolved. As death and life are 2 sides of the same coin, so are extinction and evolution. Dinosaurs, hominids, flying reptiles, and hosts of other vertebrates, invertebrates, plants, bacteria and viruses have entered, or been forced into, the black hole of extinction, whence light in the form of similar genomes never again emanates. "But these are 'natural' extinctions," you say, "not the 'untimely' extinction wrought by man, much like the difference in degree of mourning for a young man murdered as opposed to an old man slipping quietly away." Be it natural or unnatural, however, species do slip into extinction. Ecosystems recover; the biosphere continues.

Humans expend a lot of time, money and effort in evolutionarily killing a species. It takes a lot of DDT to cause Peregrine Falcons to go extinct. It is at least equally as expensive, and perhaps more so, to stay the populational decline of a species toward extinction. Species may well be important, in and of themselves, and perhaps to themselves if they could perceive their existence. But are they important to an ecosystem? Most species probably are not. That is, although a particular ecosystem may be somewhat perturbed by the removal of a species, the overall system will probably continue to exist and function in a basically similar manner. The removal of 30 California Condors from the mountains of southern California would have essentially no effect on the ecosystems that we see there today. The same can be said for the Whooping Crane, Ivory-billed Woodpecker, or any other species included in this book. In most of the world people live at levels that are substandard from the point of view of health, economies, intellectual environment, aesthetics and nutrition. They care little about the extinction of Attwater's Prairie Chicken and, indeed, would probably be glad to eat the last individual of the species.

Extinction is a worldwide phenomenon, and I have to wonder about the advisability of efforts, sometimes heroic and often costly, to save a few species of vertebrates. Do we really think that we are reversing a trend? Habitat destruction (and I feel that this is the greatest threat to the continued existence of all types of species) is progressing largely unabated throughout the world. The possibility of the spectacle of the snail darter's stopping the development of a hydroelectric plant in South America or Africa is inconceivable. Are we, are members of an environmentally aware elite, really doing a service by supporting haphazard, expensive efforts to save a few species, in effect running around trying to plug a few holes in the dike of environmental degradation as crisis after inevitable crisis develops?

A good general does not lose site of the goal. If a few battalions of soldiers must be sacrificed to win the war then it is too bad for them. The war must be won and a callous, dispassionate leader often carries the day. In a sense we are caught up in a war against environmental deterioration. The enemy is, of course, ourselves and the high standard of living maintained in the United States, high consumption societies in general, and the world's burgeoning human population.

I believe that a concerted effort is necessary to win this war. Forget about Whooping Cranes and condors. They are about gone anyway and are expensive to save. All available funds should be channeled into a global conservation master plan to attack environmental degradation on all fronts. Education, scientific data, propaganda, votes, political alliances, active and aware political leaders, personal sacrifices—these are some of the armaments to be used. Humans are really wrecking the environment. Most do not know it; most do not care. It is the duty of the informed to make them care. But I am afraid that we have underestimated the problem, misdirected our efforts, and sat back to lament the plight of the Whooping Crane. All about us is crumbling, and we rush about in a rag-tag manner saving this and saving that, and ultimately saving nothing, and perhaps becoming 1 more endangered species in the process.—MICHAEL A. MARES.

WEIGHTS OF 151 SPECIES OF PENNSYLVANIA BIRDS ANALYZED BY MONTH, AGE, AND SEX. By Mary H. Clench and Robert C. Leberman. Bulletin of Carnegie Museum of Natural History, No. 5, 1978:87 pp., $5.00.

BREEDING BIRDS OF ELEPHANT BUTTE MARSH. By Charles A. Hundertmark. New Mexico Ornithological Society Publication No. 5, 1978: 17 pp., 1 map, $1.35.

REVISED CHECK-LIST OF THE BIRDS OF NEW MEXICO. By John P. Hubbard. New Mexico Ornithological Society Publication No. 6, 1978: 110 pp., 2 maps, $2.50.—Order from Secretary, New Mexico Ornithological Society, 223 Morningside Drive, N.E., Albuquerque, NM 87108.

Wilson Bull., 91(1), 1979, pp. 163–176

PROCEEDINGS OF THE FIFTY-NINTH ANNUAL MEETING

JAMES TATE, JR., Secretary

CURTIS S. ADKISSON, Secretary-elect

At the invitation of the Brooks Bird Club, the West Virginia University and the West Virginia University Department of Wildlife Biology, the Fifty-ninth annual meeting of the Wilson Ornithological Society was held at the State 4-H Camp at Jackson's Mill, West Virginia, from 4–7 May 1978. Paper sessions and business meetings were held in the Assembly Hall and the Kanawha Room. The Executive Council met in the Walnut Room of the Jackson Lodge.

An open house and reception was held in the West Virginia Building on Thursday evening. A program on African birds was presented later the same evening by Larry Schwab. Appalachian and other nature art was exhibited by Robert L. Smith in the lounge of the Jackson Lodge.

Early morning bird walks were held on Friday and Saturday. Longer trips were taken to the Cheat-Gaudineer Region and Holly River State Park on Sunday. A spouses' tour hosted by Charles and Helen Conrad was taken to a nearby glass factory. George Breiding led a botanical walk on Saturday. Many participants spent spare moments at the historical museum on the Mill grounds.

On Friday night a barbecue was held at the outdoor picnic area, followed by a square dance in the West Virginia Building. Music was provided by the Wild Turkey String Band. The annual banquet was held Saturday night at the Mt. Vernon Dining Hall. A presidential address by Douglas A. James (see *Wilson Bull.* 90:306–308), and a talk by Maurice Brooks (see *Wilson Bull.* 90:464–467), past president of the Society, highlighted the evening.

FIRST BUSINESS MEETING

The first business meeting was called to order by President James at 0917 in the Assembly Hall. The Society was welcomed by Dale W. Zinn, Dean of the College of Agriculture and Forestry, West Virginia University.

The Proceedings of the meeting held at Mississippi State University were approved by the membership as published in *The Wilson Bulletin* (89:506–519, 1977). President James announced that Jon C. Barlow, Mary H. Clench, and Roland R. Roth would serve as the Alexander Wilson Prize committee. The nominating committee was announced as Jerome A. Jackson, chairman, Andrew J. Berger, and James R. Karr. The auditing committee was announced as James F. Ponshain and George M. Wickstrom. The standing resolutions committee was announced as Robert D. Burns, Sally Hoyt Spofford, and Sidney A. Gauthreaux.

Reports of officers and committees follow.

THE WILSON ORNITHOLOGICAL SOCIETY

REPORT OF THE TREASURER

Year Ending December 31, 1977

GENERAL FUNDS

Balance as of last report December 31, 1976			$21,443.25
RECEIPTS			
Membership Dues			
Active for 1977	$ 3,902.00		
Active for 1978	12,600.00		
Total Active		$16,502.00	
Sustaining for 1977	285.00		
Sustaining for 1978	855.00		
Total Sustaining		1,140.00	
Subscriptions to *The Wilson Bulletin*			
For 1977	1,705.00		
For 1978	6,410.00		
Total Subscriptions		8,115.00	
Advance Renewals		1,425.00	
Sales of Back Issues of *The Wilson Bulletin*		1,584.75	
Interest and Dividends on Savings & Investments			
Income from General Endowment Fund	5,933.83		
Income from G. M. Sutton Colorplate Fund	1,805.47		
Interest on Endowment Savings Account	537.23		
Interest on Regular Savings Account	61.03		
Total Interest and Dividends		8,337.56	
Royalties from Microfilming Back Issues of *The Wilson Bulletin*		192.99	
Contributions from Authors and Others		4,261.80	
Total Receipts			$41,559.10
DISBURSEMENTS			
The Wilson Bulletin (Printing & Engraving)		$33,032.98	
The Wilson Bulletin (Mailing & Maintenance)		4,203.09	
Colorplate Processing Expense		2,662.04	
Editor's Expense		1,740.00	
Secretary's Expense		338.28	
Treasurer's Expense		2,051.25	
Committee Expense		2,097.91	
President's Expense		13.00	
International Council for Bird Protection		30.00	
Miscellaneous Expense		41.62	
Total Disbursements			$46,210.17
Excess of Disbursements over Receipts			$ 4,651.07

GENERAL CASH FUND

Checking Account	
Balance in Old Kent Bank and Trust Co.,	
Grand Rapids, Michigan, December 31, 1977	$18,463.65

JOSSELYN VAN TYNE MEMORIAL LIBRARY FUND

Balance as of Last Report December 31, 1976	$ 408.21

RECEIPTS

Sale of Duplicates and Gifts	$ 1,018.77

DISBURSEMENTS

Purchase of Books	$ 896.40
Balance in Old Kent Bank and Trust Co.,	
Grand Rapids, Michigan, December 31, 1977	$ 530.58

LOUIS AGASSIZ FUERTES RESEARCH FUND

MARGARET MORSE NICE FUND

EDWARDS AND W.O.S. PAPER FUNDS

Balance as of Last Report December 31, 1976	$ 2,047.00

RECEIPTS

Contributions	$ 699.50

DISBURSEMENTS

Grant-In Aid		
To David R. Maurer	$100.00	
To Ernest Stevens	200.00	
To Dale Lewis	200.00	
To David Hendricks	200.00	
To Glen Fox	200.00	
To Douglas Mock	100.00	
Total		$ 1,000.00
Balance in Old Kent Bank and Trust Co.,		
Grand Rapids, Michigan, December 31, 1977		$ 1,746.50

AARON BAGG
STUDENT MEMBERSHIP AWARD FUND

Balance as of Last Report December 31, 1976	$ 424.00

RECEIPTS

Contributions	$ 220.00

DISBURSEMENTS

Student Membership Grants	$ 310.00
Balance in Old Kent Bank and Trust Co.,	
Grand Rapids, Michigan, December 31, 1977	$ 334.00

ENDOWMENT FUNDS

GENERAL ENDOWMENT FUND

Balance in Endowment Savings Account, Old Kent Bank and Trust Co., Grand Rapids, Michigan, as of Last Report December 31, 1976		$ 9,540.00
RECEIPTS		
Life Membership Payments		$ 17,860.00
Balance in Endowment Savings Account, Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1977		$ 27,400.00
Investment Held as of December 31, 1976		
United States Government Bonds	$ 5,084.38	
International Bank Bonds	9,495.00	
Canadian Provincial Bonds	4,056.25	
Corporate Bonds	18,610.00	
Convertible Corporate Bonds	2,000.00	
Convertible Preferred Stocks	7,997.50	
Common Stocks	55,253.13	
Uninvested Principal	2,908.76	
Total Investments		$105,405.02
Total General Endowment Fund December 31, 1977		$132,805.02

GEORGE MIKSCH SUTTON COLORPLATE FUND

Investments Held as of December 31, 1977		
International Bank Bonds	$ 1,055.00	
Canadian Provincial Bonds	4,412.50	
Corporate Bonds	9,562.50	
Common Stocks	8,900.00	
Total Investments		$ 23,930.00
Total Combined Wilson Ornithological Society Endowment Funds December 31, 1977		$156,735.02

Ernest E. Hoover, *Treasurer*

REPORT OF THE EDITOR—1977

From 1 January through 31 December 1977, 199 new manuscripts were received; 78 new manuscripts were received from 1 January through 2 May 1978. These are in addition to many revisions received during this time. The status of these manuscripts is as follows:

Status	Manuscripts received in	
	1977	1978
Published	3	0
In press	23	0
Rejected	69	9
Out to referees	1	29
Back for revision	39	17
Accepted	61	5

Decision file	1	1
Withdrawn	2	0
Forwarded to Jon Barlow	0	17

On an issue-by-issue basis, the following is the status of volumes 90 and 91:

Volume 90

- No. 1, March: 158 pp., 8 papers, 10 notes, 12 reviews. Published 19 April 1978.
- No. 2, June: pp. unknown; 12 papers, 12 notes, 7 reviews, President's page, Conservation Committee Report on management practices on National Wildlife Refuges. At the printer and on schedule for a June publication date.
- No. 3, September: pp. unknown; 9 papers, 15 notes; most copy is ready for the printer but we have no lead article with a color plate.
- No. 4, December: pp. unknown, 9 papers, 15 notes.

Volume 91

- No. 1, March: pp. unknown, 9 papers, 15 notes.
- No. 2, June: pp. unknown, 6 notes.

Rejection rate of 156 manuscripts received during 1977 and processed to some definite outcome was 44.2%. The rejection rate similarly calculated for manuscripts received thus far in 1978 has been 64.3%. Since these calculations do not include manuscripts which have been returned for revision, and since the majority of those will eventually be accepted, I also calculated a rejection rate using the assumption that all manuscripts returned for revision would eventually be accepted—this rate is 35.4% for 1977.

With approximately 200 manuscripts submitted each year (199 in 1977), approximately 100 manuscripts published each year (99 in 1977), and a rejection rate of approximately 35%, we are in trouble. This means that we will have an increase in backlog of about 30 manuscripts per year. In order to prevent an undesirable backlog we must publish more papers, reject more papers, or decrease the length of those published. I have been trying to fight the backlog problem from all three approachs. Many authors, particularly those with brief notes or those who are federal employees, have elected to pay page charges and have thus enabled us to include more articles per issue. I have tried to eliminate unnecessary verbosity, tables, and figures from manuscripts and I encourage you, when you are acting as referees, to indicate places where you feel a manuscript can be pruned. I have also attempted to be more selective in the manuscripts to be accepted, but it is difficult to reject a manuscript if referees don't do their part by recommending rejection when rejection is warranted. Often a marginal mauscript would be much more appropriate for another journal; in such cases referees would do the Society and the author a favor by making such a suggestion instead of recommending publication in *The Wilson Bulletin* after major revision.

The March 1978 issue has a series of photographs of Florida Scrub Jay young. June 1978 will feature a painting of *Piculus* heads by G. M. Sutton to accompany an article on *Piculus* variation by Luis Baptista. I have a possible plate of a new species (painted by John O'Neil) semi-promised for September—but nothing in hand. I have no leads for a color plate for December. Color plates continue to cause problems—mostly because of a lack of them. The March 1978 issue was late because I had difficulty in getting a color plate. The plate for the June issue is already at Allen Press, but in that case I have not yet received properly revised black-and-white illustrations for the lead article—hence I have not yet been able to page up the issue. Please be vigilant for appropriate color plates and accompanying articles.

Time from receipt to acceptance of papers published in volume 89 (including time needed for revision by the author) was 98.5 days for notes and 151.1 days for major papers. Time from receipt to rejection of manuscripts averaged 93.5 days. Turn-around time for both notes and papers is presently about 12–14 months from the date of acceptance to date of publication.

Last year, in an attempt to cut postage costs, I began mailing manuscripts to referees at a special 4th class rate—this worked great for about 6 months and probably saved the society $100–$150. In the past few months, however, I have been having considerable difficulty with the postal service and at least 2 manuscripts and possibly a third have been lost. Fortunately all were copies and no original figures were lost. Also, the initial mailing time for such manuscripts was usually in the range of 1–2 weeks. By the end of last year the mailing time was frequently 4–6 weeks; thus, I have abandoned the 4th class rate. As a result of our using 1st class for processing of manuscripts, the processing time should go down again but postage expenses will be high.

I have enjoyed my tenure as editor of *The Wilson Bulletin* and I appreciate the support you have given me. The job I have done, however, has involved the generous help of many. Ken Blair, Arly Allen, and Guy Dresser of Allen Press have certainly eased the burden and made my role in getting the journal out on time a lot easier. We are very fortunate to have the close association we have with Allen Press. A number of students have served as editorial assistants to me in the past four years. I have tried to expose them to all of the aspects of editing a journal—from refereeing to marking copy to proofreading—and we have all benefitted from their efforts. I feel confident that the ornithological community will find a fine editor from among them in the future. A number of individuals have helped with indexing—and I know of no more frustrating and tedious job that is appreciated so little. A good index makes a journal much more useful, and I feel that our indices in the past few years have been exceptionally thorough. Finally, the everyday work of handling manuscripts and corresponding with authors could not have been accomplished as quickly or as efficiently without the outstanding assistance of Lyda Eubanks and Vickie Bennett, our departmental secretaries.

There is one group that I haven't acknowledged enough in the past 4 years. We can't have a good journal without good referees. I am very much indebted to the 339 referees who have served the society during my tenure as editor.

Jerome A. Jackson, *Editor*

REPORT OF THE MEMBERSHIP COMMITTEE—1977

Chairman Abbot S. Gaunt submitted a report to the Executive Committee concerning progress in arranging a combined ornithological membership mailing and billing list potentially involving the Wilson Ornithological Society, Cooper Ornithological Society and American Ornithologists' Union. Dr. Gaunt also gave an informal verbal report on the current membership status of the Wilson Ornithological Society including the observation that the Society showed a net gain of about 30 members in 1977 compared to 1976.

REPORT OF THE STUDENT MEMBERSHIP COMMITTEE—1977

Letters requesting membership nominations of students interested in ornithology and inviting application from exceptional students to be considered for Aaron M. Bagg Student Membership Awards were sent to over 200 college and university faculties throughout North America. This activity resulted in 40 applications for the Bagg Award; 18 were selected as award recipients. Award recipients were announced in *The Wilson*

Bulletin (90(1):157). An additional 48 individuals were nominated for membership in the society. These nominees received a letter from the Student Membership Committee and also a letter from a group of graduate student members. The latter was designed to present the advantages of membership from the perspective of active student members. An analysis of membership trends, including study of the student nomination and awards program has been initiated by an ad hoc committee on Recruitment and Evaluation of Student Membership.

James R. Karr, *Chairman*
Roland R. Roth
Stephen M. Russell
Elliot J. Tramer

INTERIM REPORT OF THE CONSERVATION COMMITTEE—1977

The 1978–79 Conservation Committee consists of Milton Weller, Marcia M. Wilson (student), Brian R. Chapman, Laurence R. Jahn, Chandler S. Robbins, and Eric G. Bolen. The committee has taken the following actions to date:

1. Solicited materials from the WOS membership concerning difficulties in obtaining collecting permits. An announcement requesting such information was given to the Editor of *The Wilson Bulletin* for publication as soon as possible. Additional materials concerning permit problems have been obtained from Charles Sibley, Richard Banks, and Douglas James. An appropriate letter, with supporting documents, will be sent to Congressman Leggett in the near future.

2. A resolution endorsing the pending legislation on nongame birds was formulated and sent to the Resolutions Committee for action. The resolution supports the bill (H. R. 10915) using an excise tax on bird seed, feeders and houses, spotting scopes, etc. as a funding base; it is anticipated that 20–30 million dollars annually will result for nongame research and management activities with the passage of this bill.

3. The Committee's main thrust will deal with nongame matters. We initially considered sending representative states a questionnaire concerning their nongame program, exclusive of funding, in order to assess the current status of nongame activities. However, we learned that at least 2 other agencies had prepared and distributed similar questionnaires and that the subsequent response was poor enough to preclude our own intentions. Accordingly, we will now focus on the model program of the Missouri Department of Conservation, the previously collected information on nongame funding compiled by the Wildlife Management Institute, and other materials for the preparation of our final report, including recommendations. The acquisition and implementation of nongame programs on mitigating lands under the Wildlife Coordination Act will be part of our interest. A final report is anticipated by midsummer.

Eric G. Bolen, *Chairman*

REPORT OF THE LIBRARY COMMITTEE—1977

The Josselyn Van Tyne Memorial Library has, for the most part, carried on "business as usual" during 1977. Janet Hinshaw keeps our current activities in order, and finds time to catch up more and more of the loose ends that remain. These involve such long-standing problems as storage of duplicates and of "Bulletin" back issues, and questions about old subscriptions and exchanges. Perhaps it has not been sufficiently stressed that our headquarters, here at the Bird Division of the University of Michigan Museum of Zoology, handles not only the Library collections as such but also much of the special business of the "Bulletin" itself, such as orders for back issues and complete sets.

Exchanges in 1977 totaled 111—we received 139 journals, newsletters and reprints. Thirty-eight gifts and complimentary subscriptions brought the total of items received to 177.

New Book Fund transactions included the purchase of 43 new books, journals and records for the Library. From the sale of duplicate books, $200 was taken in.

The year's total of loans to members came to 85, involving 265 books, journals, photocopies, reprints and translations.

Donations added 1360 items to our holdings: 138 books, 204 periodical issues, 64 reports and pamphlets, 1 thesis and 953 reprints. Many of these will, as always, be sold as duplicates and converted into cash for the New Book Fund. The 33 donors were: R. M. Bailey, A. J. Berger (889 items, including 821 reprints), C. R. Brown, R. Butsch, Carnegie Museum of Natural History, M. L. Chamberlin, J. Cheek, J. Cooper, Dr. & Mrs. W. P. Cottrille, J. J. Dinsmore, C. P. Dau, J. A. Feduccia, N. N. Harrington (for Canadian Arctic Gas Study, Ltd.), F. Haverschmidt, M. J. Jaeger, D. W. Johnston, L. H. Kelso, W. A. Lunk, H. Mayfield, T. R. Miley, J. Miller (for Cooper Ornithological Society), D. H. Morse, W. M. Pulich, J. Schwartzkopff, W. E. Southern, P. R. Stettenheim, R. W. Storer, C. E. Tull (for Renewable Resources Consulting Service), J. A. Walker Estate (152 items, including 120 books), G. J. Wallace, L. L. Wolf, Col. L. R. Wolfe, and R. Wood (for Loon Preservation Committee).

We thank the membership for its support, and we urge that it continue—for the long-lasting benefit of everyone concerned.

William A. Lunk, *Chairman*

SECOND BUSINESS MEETING

President James called the meeting to order at 14:50 on 6 May 1978. New members were elected into the society by acclamation. The report of the Nominating Committee was read as follows by Jerome A. Jackson: President, Douglas A. James; First Vice-president, George A. Hall; Second Vice-president, Abbot S. Gaunt; Secretary, Curtis S. Adkisson; Treasurer, Ernest E. Hoover; election to Council, James R. Karr (term expires in 1979), Clait E. Braun (term expires in 1980), Sidney A. Gauthreaux (term expires in 1981); Editor, Jon C. Barlow. President James then called for nominations from the floor; there being none, a motion was made, seconded, and approved by voice vote to close nominations. James asked for and received a motion to approve the slate by acclamation, which was approved. The secretary then summarized actions of the Council at its second meeting. The 1979 meeting will be held in Omaha, at the invitation of the University of Nebraska–Omaha, from 5–8 April, 1979.

James R. Karr summarized the recommendations to Council of a special "Bite the bullet committee" on the society's financial situation. The recommendations on membership dues and page charges for publications in *The Wilson Bulletin* were approved by the membership present, and were published in *The Wilson Bulletin* (90:463, 1978). President James asked for the following Auditor's Report which was read and accepted.

AUDITOR'S REPORT

We have examined the treasurer's records, bank statements, cancelled checks, account books and other financial records of the Society covering transactions occurring during the past fiscal year. The financial status of the Society is substantially as set forth in the treasurer's report dated December 31, 1977.

Our examination has ascertained that all income has been applied to the proper funds and no expenditures have been made except as authorized.

James F. Ponshair, *Member*
George M. Wickstrom, *Member*

The final item at the second business meeting was the report of the Standing Committee on Resolutions, read by chairman Robert D. Burns. The resolutions which follow were adopted by the membership. President James had received word that a resolution concerning Bachman's Warbler and I'On Swamp would be sent to the Resolutions Committee for consideration. No request was received so that it was the consensus of the Committee to drop the matter. Had such a proposal been submitted from the floor, it was decided that the Committee would not endorse it.

WHEREAS, The Wilson Ornithological Society recognizes those natural resources collectively identified as "nongame" as a major component of our nation's fauna, and

WHEREAS, the need for detailed research and affirmative management of nongame resources is of paramount concern, and

WHEREAS, pending federal legislation proposing an excise tax on certain outdoor equipment, bird seed, and related materials may incur revenues of $20 to $30 million annually expressly for research and management of nongame species,

THEREFORE, BE IT RESOLVED that The Wilson Ornithological Society heartily endorses and supports passage of HR 10915, legislation of great importance for the enhancement of nongame resources in the United States.

WHEREAS, in 1977 The Wilson Ornithological Society resolved to oppose construction of all water projects that are detrimental to the environment, and

WHEREAS, the proposed Davis Power Project would flood one-third of the Canaan Valley, 7000 acres, plus 500 acres of Cabin Mountain, and

WHEREAS, it contains unique boreal features as well as substantial populations of deer, beaver, black bear, wild turkey, woodcock, grouse and is a major waterfowl habitat for many species of ducks and fish,

THEREFORE, BE IT RESOLVED that the Wilson Ornithological Society opposes the proposed Davis Power Project, and supports the proposed establishment of a Canaan Valley National Wildlife Refuge, and

BE IT FURTHER RESOLVED that the Society commends Governor John D. Rockefeller, IV and the West Virginia Department of Natural Resources for their support of the proposed Canaan Valley National Wildlife Refuge.

WHEREAS, Jerome A. Jackson has served with distinction as editor of *The Wilson Bulletin* from 1974 to 1978, and

WHEREAS, his infectious enthusiasm and energy have continued to improve *The Wilson Bulletin* as a fine and distinguished journal of ornithology, and

WHEREAS, the increased number of submitted papers and increased size of the Journal were handled in addition to his heavy research and teaching duties at Mississippi State University,

THEREFORE, BE IT RESOLVED that The Wilson Ornithological Society extends special thanks and appreciation for his devoted and loyal service.

WHEREAS, James Tate, Jr. has faithfully served The Wilson Ornithological Society as its Secretary since 1971, and

WHEREAS, he has diligently attended to the multitude of details which go with the responsibilities of secretary including the usual correspondence plus arranging for annual meetings, business meetings, publishing the proceedings and minutes of such meetings and keeping excellent records of the activities of the Society,

THEREFORE, BE IT RESOLVED that The Wilson Ornithological Society extends its very sincere appreciation and thanks to James Tate for his outstanding service.

WHEREAS, The Wilson Ornithological Society has returned to the State 4-H Camp at Jackson's Mill, West Virginia, for its Fifty-ninth Annual Meeting on May 4 through 7, 1978, and

WHEREAS, the scientific program and the setting at Jackson's Mill have both been superb, and the membership and friends have enjoyed and learned much because of the extraordinary efforts of the Committee on Arrangements, the Scientifie Program Committee and the Staff of Jackson's Mill 4-H Camp,

THEREFORE, BE IT RESOLVED that The Wilson Ornithological Society expresses its appreciation and thanks to the Committee on Arrangements, the Scientific Program Committee and the Camp Staff for their long and labored efforts behind the scenes which have made the Fifty-ninth Annual Meeting a superb performance.

The meeting adjourned at 15:05.

At the annual banquet the following awards and prizes were announced:

Louis Agassiz Fuertes Award
Alexis A. E. MacLean, "Kleptoparasitism as an alternative foraging strategy in immature gulls"

Margaret Morse Nice Award
David Raimist, "Vocalization patterns of endangered Palauan avifauna"

Edwards Prize
Richard Brewer and Lynda Swander, "Life history factors affecting the intrinsic rate of natural increase of birds of the deciduous forest biome" (Wilson Bull. 89:211–232)

Edwards Prize—Second Award
Wayne C. Weber and John B. Theberge, "Breeding bird survey counts as related to habitat and date" (Wilson Bull. 89:543–561)

Alexander Wilson Prize
Sheila G. Hilsenbeck, "Foraging behavior and competition in two species of southern Florida kingbirds"

PAPERS SESSION

D. McGeen, Pontiac, Michigan, *An update on cowbird-host research.*

A. A. E. MacLean, Univ. of Rochester, Rochester, New York, *An inter- and intraspecific comparison of age-related foraging ability as seen in three* Larus *species.*

K. L. Bildstein, The Ohio State University, Columbus, *Age and sex-dependent differences in hunting behavior, habitat use, and diet of Northern Harriers wintering in south-central Ohio.*

R. N. Conner, Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, Texas, *Seasonal changes in breadth of woodpecker foraging behavior.*

S. G. Hilsenbeck, Univ. of Miami, Coral Gables, Florida, *Foraging behavior and competition in two species of southern Florida kingbirds.*

D. E. Samuel and D. Wingate, West Virginia University, Morgantown, and Dept. of Agr. and Fisheries, Bermuda, *Food habits of the Kiskadee on Bermuda.*

R. Roth, Univ. of Delaware, Newark, Delaware, *Foraging behavior of mockingbirds: the effect of too much grass.*

S. F. Bailey, Museum of Vertebrate Zoology, Univ. California, Berkeley, *Foraging strategies of frugivorous birds in relation to the availability of berries.*

Elliot J. Tramer, University of Toledo, Toledo, Ohio, *Introductory remarks* to the symposium on avian resource strategies, and *Seasonal and geographic variations in foraging of migrant warblers.*

Thomas C. Grubb, Jr., Ohio State University, Columbus, *Branch selection by foraging chickadees and titmice in a controlled laboratory "habitat."*

Steven D. Fretwell, Kansas State University, Manhattan, *Foraging in seed-eating birds.*

Robert C. Whitmore, West Virginia University, Morgantown, *Multivariate methods in the analysis of avian resource use.*

Frank B. Gill, Academy of Natural Sciences, Philadelphia, Pennsylvania, *Foraging behavior of nectar-feeding birds.*

James D. Kushlan, Everglades National Park, Homestead, Florida, *Resource use patterns in wading birds.*

Douglass H. Morse, University of Maryland, College Park, *Feeding systems in birds: a synthesis.*

D. Howes-Jones, Royal Ontario Museum, Toronto, *Structural, functional, and information relationships among the call notes of the Warbling Vireo.*

S. R. Borecky, Univ. of Pittsburgh, Pittsburgh, Pennsylvania, *The appendicular myology and evolutionary relationships of the Artamidae.*

R. J. Raikow, Univ. of Pittsburgh, Pittsburgh, Pennsylvania, *The relationships and taxonomic position of* Nephelornis oneilli.

G. D. Bentz and R. L. Zusi, National Museum of Natural History, Smithsonian Institution, Washington, D.C., *Evolution of the humeroulnar pulley in hummingbirds.*

J. D. Rising and G. F. Shields, Univ. of Toronto, Toronto, Ontario, Canada, and the Univ. of Alaska, College, Alaska, *What selects for chromosomal polymorphisms in birds?*

T. L. Lloyd-Evans, Manomet Bird Observatory, Manomet, Mass., *Postjuvenal molt of Massachusetts House Finches.*

J. C. Barlow, Royal Ontario Museum, Univ. of Toronto, Toronto, Ontario, Canada, *Behavioral, ecological and morphological responses of the* Empidonax traillii/alnorum *complex in syntopy.*

M. H. Clench, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, *Recent discoveries on the winter habitat of Kirtland's Warbler.*

K. G. Beal, The Ohio State University, Columbus, *A year-round field study of weather-dependent behavior of the Roadrunner. I. Winter.*

W. M. Shields and K. L. Bildstein, Ohio State University, Columbus, *Behavioral Interactions between bats and Common Nighthawks at a localized food source.*

R. J. McPherson and R. D. Brown, the Univ. of North Carolina at Charlotte, Charlotte, *Responses of some passerines to the call and location of the Screech Owl* (Otus asio).

P. D. Caprio, Miami Univ., Oxford, Ohio, *Effects of Sevin on egg and eggshell characteristics of Coturnix quail* (Coturnix coturnix japonica).

J. W. Via, Virginia Polytechnic Institute and State University, Blaeksburg, *Eggshell quality improvement in Ospreys from the Chesapeake Bay.*

D. Lank, Cornell Univ., Ithaca, New York, *Migratory orientation and activity in sandpipers.*

J. A. Jackson, Mississippi State Univ., Mississippi State, *Age characteristics of Red-cockaded Woodpeckers.*

E. D. Michael and T. A. Losch, West Virginia Univ., Morgantown, *Visibility of birds along interstate highways.*

D. Klem, Jr., Southern Illinois Univ., Carbondale, *Collision between birds and windows.*

G. R. Myers and D. W. Waller, Kent State Univ., Kent. Ohio, *The effects of helpers at the nest in Barn Swallows.*

R. W. Dexter, Kent State Univ., Kent, Ohio, *The fate of "helpers at the nest" with nesting Chimney Swifts.*

L. A. Lyon and D. F. Caccamise, Rutgers, the State Univ. of New Jersey, New Brunswick, *Spatial and temporal patterns of roosting behavior in mixed assemblages of blackbirds and starlings.*

M. A. Springer, Miami Univ., Oxford, Ohio, *Growth and development of Red-tailed Hawks in central Ohio.*

J. J. Potyraj, Towson State Univ., Baltimore. Md., *Effects of investigator presence on the breeding success and nestling growth of the Cattle Egret.*

D. F. Werschkul, Mississippi State Univ., Mississippi State, *Adaptive significance of nestling development in the Little Blue Heron.*

E. H. Alforn, Brigham Young Univ., Provo, Utah, *An adaptive advantage for early nesting in White-faced Ibis* (Plegadis chihi).

S. Sabo, Cornell Univ., Ithaca, New York, *Community description of a subalpine avifauna.*

J. R. Karr, Univ. of Illinois, Champaign, Ill., *On the stability of tropical forest avifaunas.*

J. Keller and C. R. Smith, New York Coop. Wildlife Res. Unit and Lab of Ornith., Cornell Univ., Ithaca, New York, *Effects of a late spring controlled burn on breeding birds in central New York.*

L. B. McArthur, West Virginia University, Morgantown, *Passerine community structure in a forest: the effects of two silviculture practices.*

S. A. Briggs and J. H. Criswell, Audubon Naturalist Society of the Central Atlantic States, Washington, D.C., *Comparison of population trends between all-year and migratory breeding birds, 1947–1977, in three Washington, D.C. area study tracts.*

Charles Smith, Laboratory of Ornithology, Cornell Univ., Ithaca, New York, *Special Report: The role of the amateur in ornithology.*

ATTENDANCE

ARKANSAS: *Fayetteville*, Douglas James.

CALIFORNIA: *Berkeley*, Stephen F. Bailey. Karen Bailey.

COLORADO: *Fort Collins*, Clait E. Braun; *Golden*, Jim Tate.

DELAWARE: *Newark*, John T. Linehan, Roland Roth.

DISTRICT OF COLUMBIA: *Washington*, Richard C. Banks, G. D. Bentz, William S. Clark, Richard Zusi.

FLORIDA: *Homestead*, James Kushlan; *Lehigh Acres*, Maxine C. Kiff; *Miami*, Ronald Gaby, Shela Gaby, Susan G. Hilsenbeck; *Winter Haven*, Peggy MacQueen.

ILLINOIS: *Carbondale*, Daniel Klem, Jr.; *Champaign*, James R. Karr.

INDIANA: *Hanover*, J. Dan Webster, Juanita Webster.

KANSAS: *Manhattan*, Stephen Fretwell.

MAINE: *Brunswick*, Bibbo Whitman, Burt Whitman; *Wayne*, Olin Sewall Pettingill, Jr.

MARYLAND: *Baltimore*, Charles Davis, James J. Potyraj; *Bethesda*, Shirley A. Briggs, Fred G. Evenden, Mildred J. Evenden, Eilene Williams; *Chestertown*, D. A. Mendinhall; *College Park*, Douglass H. Morse; *Laurel*, Stanley H. Anderson, Brian W. Cain, Jay M. Sheppard; *Towson*. Gladys Hix Cole, Phillip D. Creighton.

MASSACHUSETTS: *Petershorn*, John C. Fiske, Rosalie Fiske; *Plymouth*, Trevor Lloyd-Evans; *Topsfield*, Ralph D. Scott.

MICHIGAN: *Ann Arbor*, Janet G. Hinshaw, Stephen H. Hinshaw, Ronald Orenstein, Louise S. Storer, Robert W. Storer; *Grand Rapids*, Ernest Hoover; *Howell*, Steven M. Goodman, Julie Wolinski, Richard A. Wolinski; *Jackson*, Marie Whiting, Robert A. Whiting; *Muskegon*, Thaddeus A. Grudzien; *Pleasant Lake*, Hubert P. Zernickow, Norene E. Zernickow; *Pontiac*, Daniel S. McGeen, Jean McGeen.

MISSISSIPPI: *Mississippi State*, Dwight Cooley, Jerry Jackson, Bette J. Schardien, Wayne C. Weber, Wendy Weber, David F. Werschkul, Sue Werschkul.

MISSOURI: *St. Louis*, Margaret D. Feigley, Lillian Nagel.

NEBRASKA: *Omaha*, Roger S. Sharpe.

NEW JERSEY: *Bound Brook*, Charlotte A. Conn, Robert C. Conn; *Englishtown*, Donald F. Caccauiise, Rita Caccauiise; *Highland Park*, Michael Combardo; *Mt. Holly*, Katherine G. Davis, Price Davis; *New Brunswick*, Harry W. Power; *Parlin*, Allen A. Lubchansky; *Somerset*, Linda Lyon.

NEW YORK: *Ithaca*, John Guarnaccia, R. J. Gutierrez, David Lank, Helen S. Lapham, Jeff Keller, Steve Sabo, Charles R. Smith; *Oswego*, George R. Maxwell; *Phoenix*, Cathie A. Baumgartner, Roy S. Slack; *Rochester*, Alexis A. E. MacLean.

NORTH CAROLINA: *Carrboro*, Ken Meyer; *Chapel Hill*, Helmut C. Mueller, Patricia G. Parker; *Charlotte*, Richard D. Brown, David Drye, Roger McPherson, Sally Stenhouse; *Lincolnton*, Roger McPherson; *Linville*, Margery Plymire.

OHIO: *Burton*, Robert McCullough; *Columbus*, Kathleen G. Beal, Roger E. Beal, Kay Broschat, Timothy Broschat, Jan Crook, Abbot S. Gaunt, Sandra L. Gaunt, Rosemarie S. Gnam, Tom Grubb, William Shields, Andrew D. Thompson, Jr.; *East Liverpool*, John Laitsch, Nevada Laitsch; *Gambier*, Robert D. Burns; *Kent*, Jean Dexter, Ralph W. Dexter, Wayne C. Zipperer; *Lakewood*, Nancy Klamm, William A. Klamm; *Oxford*, Mark A. Springer; *Toledo*, Tom Kemp, John M. McCormic, Elliot J. Tramer; *Urbana*, Esther C. Conboy; *Youngstown*. John E. Holzback.

PENNSYLVANIA: *Bloomsburg*, Robert M. Ruhe; *Bridgeville*, Ben Pinkowski, Phyllis Pinkowski; *Canonsburg*, Donna M. Borecky, Stephen R. Borecky; *Chester Springs*. Babs Street, Phillip B. Street; *Clarksville*, Ralph K. Bell; *Edinboro*, Don Snyder; *Indiana*, Robert E. Merritt; *Kempton*, Jim Brett; *New Florence*, Daniel C. Butler; *Philadelphia*, Frank B. Gill; *Pittsburgh*, Harry K. Clench, Mary H. Clench, Ruth Ernsberger, Jay Loughlin, Maria Morlion, Ellen S. Parkes, Kenneth C. Parkes, Robert J. Raikow; *Turtle Creek*, Marie Crock; *Washington*, Roy A. Ickes.

SOUTH CAROLINA: *Chester*, Elizabeth S. Henze, W. Cornwell Stone; *Clemson*, Richard F. Harlow, Anna E. Ross.

TENNESSEE: *Knoxville*, Jackie McKitrick, Charles P. Nicholson, Thomas Smith; *Martin*, David Pitts, Marion Pitts; *Maryville*, Ralph J. Zaenglein.

TEXAS: *Corpus Christi*, Brian R. Chapman; *Nacogdoches*, Richard N. Conner, Brian Locke.

UTAH: *Provo*, Emmett H. Alford.

VERMONT: *South Londonderry*, Betty Downs.

VIRGIN ISLANDS: *St. Thomas*, David Nellis.

VIRGINIA: *Blacksburg*, Curtis S. Adkisson, Deborah Berrier, Robert L. Patterson, Jr., Jerry W. Via; *Great Falls*, Dale H. Clayton; *Harrisonburg*, Elwood Fisher, Charles W. S. Ziegenfus; *Scottsville*, Fred Whiteside, Lina S. Whiteside; *Sweet Briar*, Ernest P. Edwards, Mabel T. Edwards; *Virginia Beach*, Douglas S. Davis; *Williamsburg*, Keith L. Bildstein, Mary Leitschuh.

WEST VIRGINIA: *Bethany*, Albert R. Buckelew, Jr.; *Buckhannon*, Gigi Aiken, Maxine Thacker; *Charles Town*, Dorothy H. Caperton; *Charleston*, Anne Shreve, Harvey Shreve; *Chester*, E. R. (Pete) Chandler, Elizabeth D. Chandler; *Comfort*, Clifford E. Coon, Linnie M. Coon; *Elkins*, Eugene E. Hutton, Joseph C. Rieffenberger, Mary Rieffenberger, Jo Lane Stern, Caroline Wilson; *Franklin*, Carolyn Ruddle; *French Creek*, Virginia Bly Hoover; *Hinton*, A. G. (Andy) Timberlake, Kathlene Timberlake; *Huntington*, Libby McIntyre, Harry E. Slack; *Inwood*, Clark Miller; *Middlebourne*, Edna Gregg; *Montgomery*, Irvine D. Prather; *Morgantown*, George Breiding, John S. Castrale, George Hall, Tanya Hall, Dick Kimmel, Dennis Krusac, Kathy McArthur, Laurence B. McArthur, Edwin D. Michael, David Mindell, James M. Morash, John Noullet, David E. Samuel, Robert L. Smith, Robert L. Smith, Jr., Ellen R. Snyder, Debbie Tucker, Paul Wackenhut, Leslie Whitmore, Robert C. Whitmore, Tom Wray, B. Zimmerman; *Ona*, Leon P. Wilson; *Parkersburg*, Marion Means; *Shepherdstown*, F. W. Sturges; *Sistersville*, Gladys M. Murrey; *So. Charleston*, George Koch, Laura Koch; *Triadelphia*, Chuck Conrad, Helen Conrad, Glen Phillips; *Weirton*, Bob Rine, George Rine; *Weston*, Brete Griffin; *Wheeling*, Mary C. Becker, Lavania Moore.

ONTARIO: *Hamilton*, Daryl Howes-Jones, James S. Pringle; *Toronto*, Jon C. Barlow, Margaret May, James D. Rising, Trudy L. Rising, Shirley J. Thompson.

NEW BRUNSWICK: *Sackville*, Peter W. Kicklin.

FOREIGN COUNTRIES: *Kenya*, Larry T. Schwab.

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

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THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—George A. Hall, Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506.

First Vice-President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

Second Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Clait E. Braun (term expires 1980); Sidney A. Gauthreaux, Jr. (term expires 1981); Richard C. Banks (term expires 1982).

Membership dues per calendar year are: Active, $14.00; Student, $10.00; Sustaining, $20.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 104 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to "The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan." Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically.

THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publicaton, Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

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A pair of Royal Sunangels *(Heliangelus regalis)*, a new species of hummingbird from Peru. Painting by John W. Fitzpatrick.

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A NEW SPECIES OF HUMMINGBIRD FROM PERU

JOHN W. FITZPATRICK, DAVID E. WILLARD AND JOHN W. TERBORGH

In June 1975, during a brief avifaunal survey of the previously unexplored Cordillera del Condor in northern Peru, we encountered a common, small, midnight-blue hummingbird occupying the brushy slopes bordering moist cloud forest. The single specimen we obtained, a sub-adult male, matched no known species and even its generic affinities were uncertain. Returning to the site in July 1976, we collected a small series of this spectacular hummingbird, including several females. The species represents a distinctive new member of the genus *Heliangelus* (the sunangels), as described below (see frontispiece).

Heliangelus regalis sp. nov.

ROYAL SUNANGEL

HOLOTYPE.—American Museum of Natural History no. 823987; adult male from the Cordillera del Condor, above San José de Lourdes, dept. Cajamarca, Peru 5° 02′ S, 78° 51′ W, elevation 1950 m; collected 14 July 1976 by J. W. Fitzpatrick.

DIAGNOSIS.—A small-bodied, straight-billed, sexually dimorphic trochiline with an elongated, deeply forked tail. Entire plumage of adult males deep blue-black, showing no trace of green iridescence and no gorget. Male most similar to *Eriocnemis nigrivestis*, but lacking leg puffs, nasal operculum mostly exposed (not covered by compressed feathers as in *Eriocnemis*), tail much longer and deeply forked, and lacking bright iridescence on gorget, rump, and undertail coverts. Female closest to *Heliangelus mavors*, but distinguished from all female *Heliangelus* by elongated and deeply forked, entirely iridescent, metallic blue tail, equally bright on both surfaces; combined with buffy underparts interrupted by a pale pectoral band.

DISTRIBUTION.—Known only from the vicinity of the type locality: in the dept. Cajamarca, Peru, at elevations from 1950 to 2200 m on the southern extremity of the Cordillera del Condor, east of the Rio Chinchipe valley; range probably extends northward on this mountain ridge along the border of Peru and Ecuador.

DESCRIPTION OF HOLOTYPE.—Entire body plumage, including upper and undertail coverts, all wing coverts, and innermost secondaries, deep violet-blue, slightly bluer and much darker than Spectrum Violet (capitalized colors are from Smithe 1975); body plumage slightly iridescent throughout, appearing deep purple to nearly black in poor light; brighter iridescence of forecrown approaches Cyanine Blue. Outer secondaries and all primaries blackish with faint violet iridescence; a few tiny feathers along the alular region tipped Tawny; thighs and proximal half of tarsus feathered dark blue as body; small, semi-concealed patch of downy white feathers on crissum. Rectrices entirely dark Spectrum Violet, slightly bluer basally and on outer webs, and with bright, metallic blue iridescence on both dorsal and ventral surfaces. Tail long and deeply forked, outermost rectrices 1.9 times longer than innermost; distal half of outer 2 pairs of rectrices bowed slightly inward. Culmen feathered nearly to anterior end of nasal operculum, these feathers entirely covering the operculum over about ⅓ of its length. Soft parts colors in life: bill and feet black, irides dark brown.

MEASUREMENTS (mm) OF HOLOTYPE.—Wing chord 53.2, outermost rectrix 55.0, innermost rectrix 29.5, culmen (from anterior end of operculum) 13.8; weight, 3.7 g.

SPECIMENS EXAMINED.—Ten males, 6 females from the type locality (AMNH 2 ♂, 1 ♀; LSUMZ 4 ♂, 3 ♀; MCZ 3 ♂, 1 ♀; FMNH 1 ♂, 1 ♀).

REMARKS

Description of allotypes.—Six females were collected from the type locality. The crown, mantle, wing coverts, rump and uppertail coverts of all females are dark, oily green, with iridescence varying between specimens from deep blue to bronzy. The upper tail coverts of a few specimens are bluer than the back and rump. Remiges are dusky, showing little iridescence. A narrow superciliary, an indistinct malar streak, and the entire underparts are rich Cinnamon, varying in intensity between specimens but always darkest on the lower throat and on the belly. Underparts are mottled to varying degrees with dark, bronzy-green discs, which are small and arranged along indistinct longitudinal rows on the chin and throat (see frontispiece and Fig. 1). A broad, pale buffy breast band separates the smaller throat spots from larger and more numerous discs on the breast and flanks. In a few specimens the posterior border of the breast band is entirely defined by a broad row of these discs. The belly is free of dark spots in all specimens. The downy crissum is white as in males, and the undertail coverts are dusky, edged Cinnamon. All but the central pair of rectrices are deep, metallic blue, iridescent on both surfaces as in males. The central rectrices of 4 of the 6 females show a greenish sheen near the base. The outermost pair in 5 specimens shows a barely discernible whitish tip, especially on the outer web. The tails of females are shorter and less deeply forked than in males (see Table 1). One specimen (FMNH no. 299434) had poorly developed ovaries. Its buffy throat is entirely mottled with pale gray, and lacks the distinct, bronzy-green spots present on the other specimens. Its breast band is paler than in the remaining females, and the dark discs on breast and flanks are poorly defined. These features probably characterize young females. Soft part colors in life resemble those of the holotype.

TABLE 1

MEASUREMENTS (MM) OF *HELIANGELUS REGALIS* FROM THE TYPE LOCALITY

	Adult males (N = 5)			Subadult males (N = 5)			Females (N = 6)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Wing chord	53.4	0.9	52.2–54.5	52.8	1.3	51.0–54.5	50.7	0.6	50.0–51.6
Exp. culmen	13.7	0.3	13.4–14.2	13.4	0.4	13.0–14.0	14.3	0.9	13.2–15.8
Outer rectrix	52.4	2.2	50.5–55.0	47.3	1.7	46.0–50.0	40.3	1.2	39.5–42.0
Central rectrix	27.9	1.2	26.5–29.5	27.9	1.0	26.5–29.0	27.0	1.5	26.0–28.0
Fork depth[1]	1.9		1.8– 1.9	1.7		1.6– 1.8	1.5		1.4– 1.6

[1] Fork depth = outer rectrix length/central rectrix length.

Variation among males.—The 10 males, all collected between 20 June and 23 July, fall into 2 plumage categories. Five specimens, including the holotype, are uniformly iridescent midnight blue over the entire body. Two of these specimens show a thin, concealed band of pale buffy marks on the breast, probably homologous to the females' breast bands. Otherwise little color variation is evident among these presumed adults. The remaining 5 specimens, apparently subadults, show varying amounts of iridescent dark green on the crown, mantle, rump and flanks, along with distinct Tawny tips on blue or blue-green feathers of the lower breast, posterior flanks, and belly. The amount of this buffy scaling varies directly with the extent of green on the upperparts. One specimen (MCZ no. 330694) is entirely green above, and shows a faint breast band of buffy scaling, suggesting the female pattern. In this specimen, typical midnight blue feathers appear only along a medial stripe down the throat and irregularly across the lower breast. This and 3 other subadult males show some active molt. As judged from these subadults, the emergence of dark blue feathers apparently begins on the throat, followed by emergence on the crown, mantle and lower breast. The auriculars, nape, lower back and belly retain subadult coloration the longest. The outermost rectrices of these subadult males are significantly shorter than those of the adults (means of 47.3 vs 52.4 mm), although they still are longer than those of females (see Table 1). Wing and bill lengths are similar between the 2 age classes.

Systematic relationships.—Although *regalis* is a peculiar and distinctive species, its inclusion in the genus *Heliangelus* is supported on a number of counts. Among sexually dimorphic, straight-billed hummingbirds the unusual combination of a speckled throat and a dark-bordered pale breast band in the female is found only within *Heliangelus* (see Fig. 1). Indeed, the entire

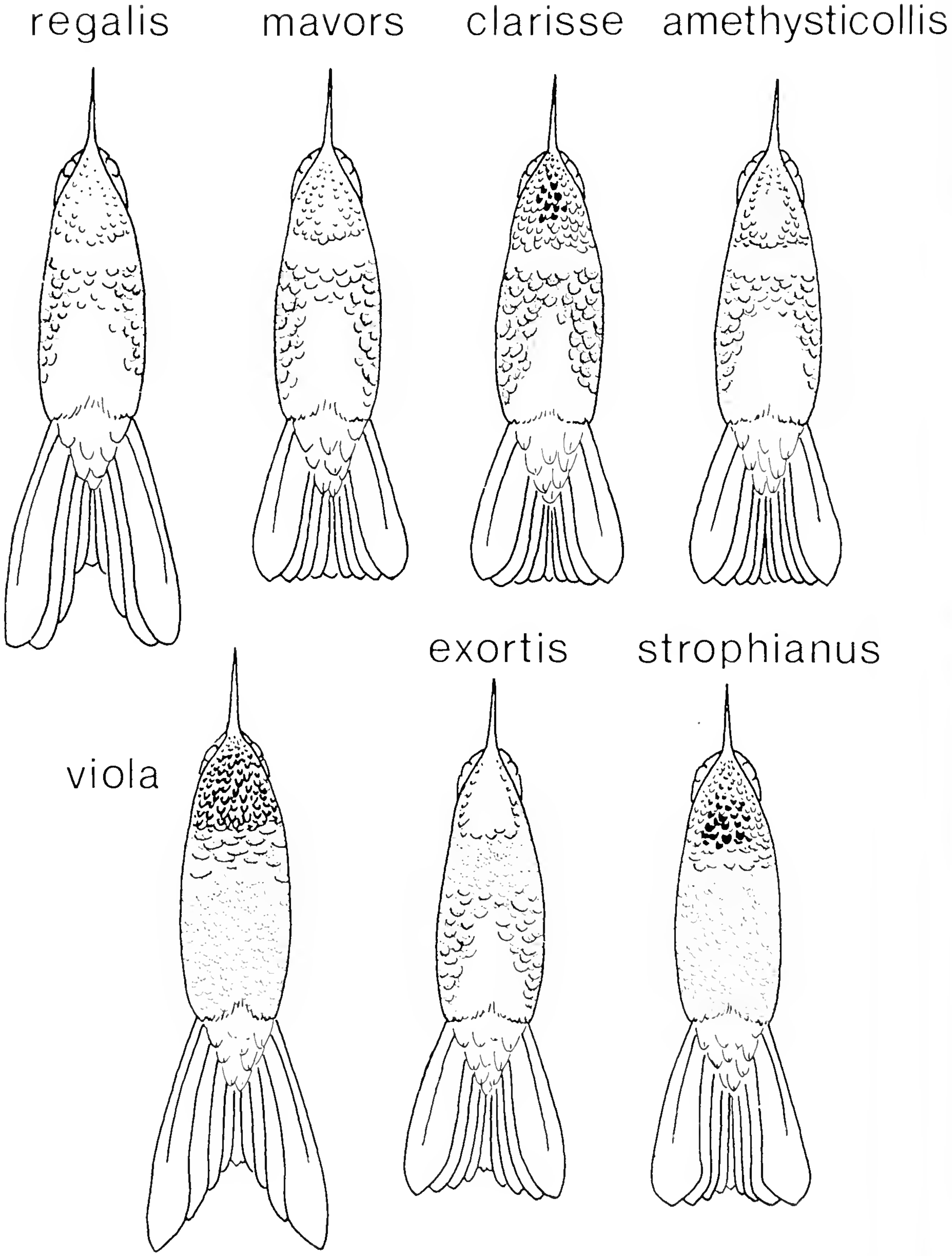

FIG. 1. Ventral patterns and tail forms of *Heliangelus* females, including *H. regalis*. *H. micrastur* female resembles *exortis*, and *H. spencei* resembles *amethysticollis*. Note similarity between *regalis* and *mavors*.

underparts of female *regalis* closely resemble those of female *H. mavors* (Orange-throated Sunangel), differing only by a paler breast band and slightly darker, less numerous blue-green spots and discs. As shown in Fig. 2, the relative bill length, nostril feathering, and well delineated nasal operculum of *regalis* all fall within the range of variation among *Heliangelus* species. Sabre-shaped outer rectrices in both males and females, faintly tipped grayish or white in the latter, characterize all species of *Heliangelus*. Elongation of the outer rectrices into a deeply forked tail, while reaching an extreme in *regalis*, is found in *H. exortis*, *micrastur* and especially *viola* (Tourmaline, Little and Purple-throated sunangels, respectively; see Fig. 1). In all species of *Heliangelus*, including *regalis*, the proximal half of the tarsus is sparsely feathered. Tarsal plumes, which characterize the adjacent genus *Eriocnemis* (the pufflegs), are entirely lacking. This distinction is important in that the male *regalis* superficially resembles several species of *Eriocnemis* more than any species of *Heliangelus*. All species of *Eriocnemis* also possess iridescent chins and undertail coverts, as well as compressed nostril feathers that entirely conceal the operculum. These features are lacking in *regalis* and its congeners.

The affinities of *regalis* within *Heliangelus* are not clear. Unlike the monochromatic male *regalis*, males of all previously known *Heliangelus* have well defined, brilliantly iridescent violet or orange gorgets that contrast with a deep green head and body plumage. In 4 of these 7 species (*mavors*, *clarisse*, *amethysticollis*, *strophianus* following Peters [1945]; Orange-throated, Longuemare's, Amethyst-throated and Gorgeted sunangels, respectively) the gorget is bordered below by a white pectoral band, appearing as a white or buffy band in the females (see Fig. 1). The presence of this breast band in female *regalis* suggests that the new form is closest to this species group. The extreme similarity between females of *regalis* and *mavors* was mentioned above. However, male *mavors* shows a well developed, fiery-orange gorget and forecrown. Its body plumage is the palest green of any in the genus, and its broad, squared tail is bronzy-green and pale-tipped. Thus, if *regalis* is indeed closest to this species as suggested by the appearance of the female, it has undergone a dramatic differentiation in which the male converged upon several more distant relatives. The elongated, narrow, metallic blue tail in both sexes of *regalis*, equally iridescent on both surfaces, is suggested only in *H. strophianus* (sexes similar) and *viola* (very large, dark green female lacks a breast band). Confirmation of *regalis*' exact position in *Heliangelus* may be possible using anatomical comparisons, but the necessary specimens are presently unavailable.

Behavior.—Both male and female *H. regalis* showed a distinct preference for nectar from 1 species of flowering melastome (*Brachyotum quinquenerve*)

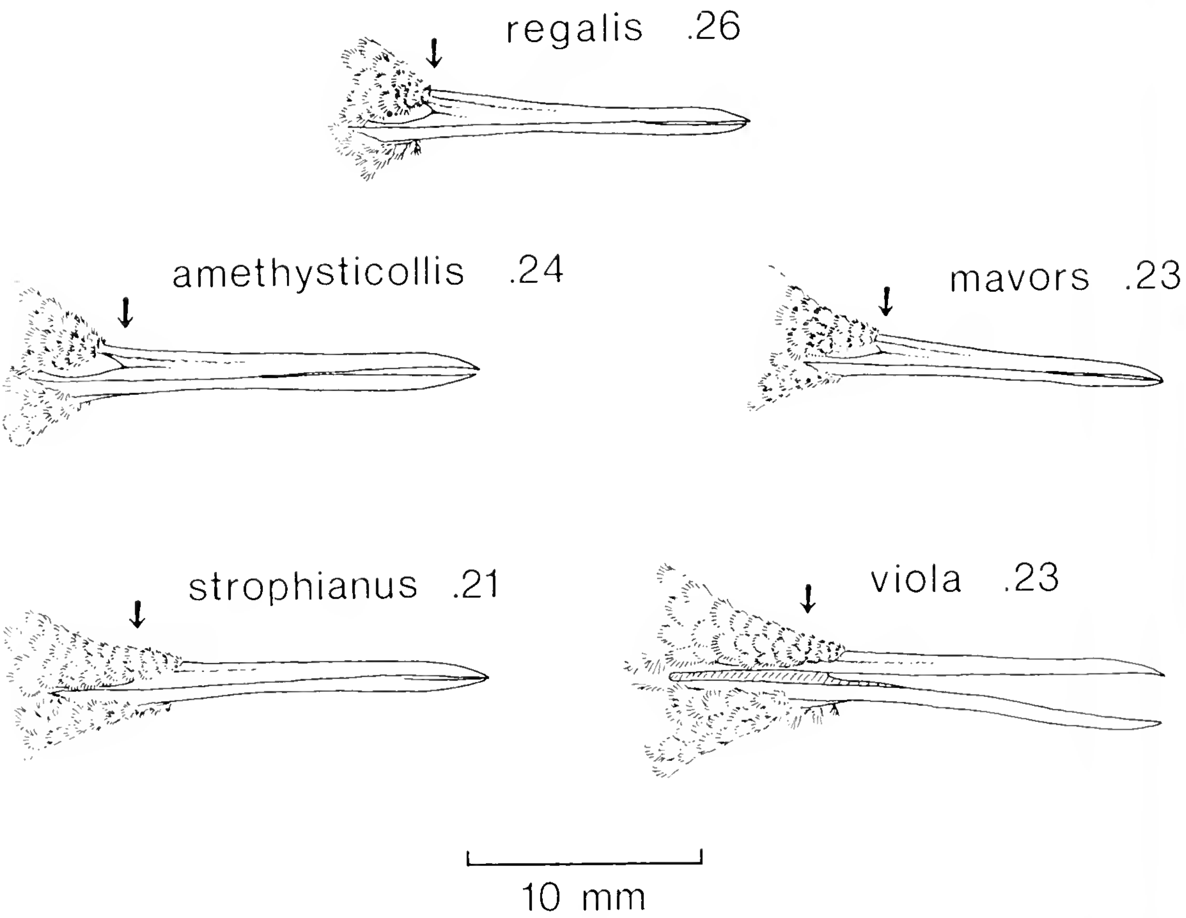

FIG. 2. Bill shape, nostril feathering, and nasal operculum characteristics in *regalis* and some representative *Heliangelus.* Small arrows show the position of the anterior end of operculum in relation to the nostril feathering. Ratio of exposed culmen to wing length is shown for each species illustrated.

during June and July. *Brachyotum,* a low shrub, has abundant flowers arranged serially along multiple stems. Its deep purple petals form a tubular corolla that hangs vertically (see frontispiece), forcing the foraging hummingbird to hover directly below and point its bill straight upward to retrieve the nectar. This plant, which forms dense stands, is an abundant component of the brushy habitat of *H. regalis,* and the genus is known to be an important food source for hummingbirds in northern Peru (Wurdack 1965). Although the most common single-flowering species in June and July, *Brachyotum* was not the only flower available at this site. At least 2 other melastomes (including *Tibouschina ochypetala*) were in full flower, along with 2 common, shrubby Compositae and several other unidentified plants. Nevertheless, nearly all of *H. regalis*' flower visits we observed were at *Brachyotum.* Individuals frequently could be seen travelling systematically from flower to flower within clumps of *Brachyotum,* usually at heights of 0.5 to 2 m within dense foliage.

At an estimated 25% of the flower visits we observed (N = ca. 200), *H. regalis* fed on nectar by perching on the stem below the flower, rather than hovering. Nectar was invariably taken through the open end of the corolla. All observers present agreed that its habit of perching to feed seemed more regular than in other hummingbirds in our experience. Whether or not this habit results from the heavy use of a short, vertically hanging inflorescence remains unknown. *H. regalis* also frequently forages for small insects. Individuals sally outward or upward several m from an exposed perch to snatch aerial prey, and usually return to the same perch.

H. regalis was highly territorial during the season we were present. When not foraging, individual males could be found sitting quietly on exposed perches near or over the top of the shrubby vegetation, and single males regularly returned to favored perches. Male-male chases were common. Chases were accompanied by a series of high-pitched *tick* notes, presumably given by the aggressor. Often these vocalizations merged into sweeter notes, whistled with an upward slur. Females occasionally uttered these same notes during long flights away from a flower clump after foraging. We estimated the territory sizes of males to be about 40–50 m in diameter, and all such territories contained good stands of *Brachyotum* in full bloom.

Two kinds of stereotyped display behavior were observed. (1) Especially just after dawn, a male was occasionally seen perched on an exposed twig up to about 6 m high, uttering a series of high-pitched, warbled, "tinkling" notes lasting 3 sec or more. This series ended with a long flight out from the perch, during which the bird traced a circle of varying diameter up to about 10 m before returning to the perch. This circular flight was then repeated on the opposite side of the perch, resulting in a "figure 8" flight pattern with the perch at the center. While flying the bird uttered the single *tick* notes described above, but upon landing at the perch he resumed the "tinkling" series of sweet whistles. (2) A male-female display was observed once by Gary R. Graves, who has kindly provided his description for our use. The following account is quoted from his notes:

> Initially a pair [of *regalis*] was foraging around the walls of [a vine-covered sinkhole] and in the surrounding shrubs along the rim. Both male and female were observed perching on a rootlet, making frequent sallies to capture tiny flying insects . . . . Three times a male was seen to displace a female from a perch. An adult male displaced an immature male once . . . . After an unseen but heard confrontation in nearby thick bushes, 2 males and 2 females appeared at the 'favorite' perch halfway down the sink wall. One pair remained only about 15 sec and then flew quickly away with a series of rapid chipping notes. The remaining pair sat quietly for another 20 or 30 sec and then flew to a

> densely branched, but thinly leaved shrub. The female remained on one perch, silently, while the male . . . changing positions above the female every 10 to 15 sec, fanned his tail, held his bill vertically, and raised his wings. While in this posture, with wings and tail flicking and vibrating rapidly, the male delivered a high-pitched, jumbled series of notes 2 to 3 sec long, repeated every 3 to 4 sec. This display lasted about 2 min and ended when the female flew off.

Upon alighting on a twig, *H. regalis* habitually holds its wings out-stretched, and occasionally quivers them slightly, before folding them. This motion is even more conspicuous and exaggerated in *H. amethysticollis.*

Breeding and molt.—As suggested by the display activities described above, *regalis* appeared to be actively breeding during our second visit, from 12 to 31 July 1976, coinciding with the onset of a relatively dry season. Males were far more visible than females during this period, suggesting that many females may have been incubating. No nests were located, but 4 of 5 adult-plumaged males, and 1 subadult specimen, showed swollen testes. Two of the 6 females showed enlarged follicles indicative of breeding condition. As mentioned above, light body molt is evident on 4 of the 5 subadult males. One adult male and at least 4 females also show body molt, but no wing or tail molt is present on any specimen.

Habitat and ecology.—The type locality of *Heliangelus regalis* is the same as that described and mapped in Fitzpatrick et al. (1977) for the Bar-winged Wood Wren (*Henicorhina leucoptera*). The Cordillera del Condor is a low, narrow mountain ridge that forms a border between Peru and southeastern Ecuador over most of its length. The ridge is separated from equivalent elevations on the main Andes to the west by about 40 km. At its southern extremity, entirely within Peru, the ridge reaches an elevation of about 2850 m, where it is capped by a dense but stunted cloud forest growing on a leached, desiccation-prone sandstone substrate. Our camps were placed at several elevations near the southernmost edge of this moist forest, along a mule trail leading eastward over the ridge from San José de Lourdes. To the south, the forest gives way abruptly to a mosaic of dense, brushy hillsides, grazed and frequently burned grassland, and black-water bogs in the shallow valleys between hills.

H. regalis appeared to be most numerous in the brushy slopes bordering the forest edge and along steep ravine banks, at elevations from 1950 m to 2200 m. In these sites the vegetation is characterized by abundant melastomes (at least 3 common species) and an undergrowth containing Ericaceae and large stands of bracken ferns. The brush is extremely dense up to 1 or 2 m in height, and reaches heights of 4 to 5 m along ravines and near the forest border. The hummingbird was occasionally sighted, and once mist-netted, inside the forest in areas where sparse canopy permitted a proliferation of understory plants. The open bogs and burned pastures to the south of the forest edge appeared not to be visited by *Heliangelus regalis*. Other hummingbirds mist-netted or observed at this elevational zone were, in order of decreasing abundance: (1) interior forest: Speckled Hummingbird (*Adelomyia melanogenys*), Booted Racket-tail (*Ocreatus underwoodii*), Bronzy Inca (*Coeligena coeligena*), Long-tailed Sylph (*Aglaiocercus kingi*), Chestnut-breasted Coronet (*Boissonneaua matthewsii*), Whitetip (*Urosticte benjamini*) and Green-fronted Lancebill (*Doryfera ludoviciae*); (2) open brush and bogs: Green Violetear (*Colibri thalassinus*), Green-tailed Trainbearer (*Lesbia nuna*) and Sparkling Violetear (*Colibri coruscans*). In the dense brush at about 2000 m, *Heliangelus regalis* was outnumbered only by *Colibri thalassinus*.

Our highest camp was placed atop a vertical precipice overlooking the Rio Chinchipe valley to the west, at an elevation of 2450 m. This site, about 2 km NNE of the lower camps, is entirely forested up to the edge of the rock face. At this elevation, *Heliangelus regalis* appeared to be absent, while *H. amethysticollis* was the most common hummingbird along the forest border at the edge of the cliff. Thus the new species may be ecologically replaced at upper elevations by a congener, as is typical of many Andean bird species including other hummingbirds (Terborgh 1971, Terborgh and Weske 1975). In the forest, Collared Incas (*Coeligena torquata*) appeared to replace *C. coeligena* in a similar fashion between 2200 and 2450 m.

So far as is known, *Heliangelus regalis* is restricted to forest edge habitats at middle elevations of the isolated Cordillera del Condor. The existence of many endemic species and subspecies on this ridge amidst a somewhat depauperate bird fauna (Fitzpatrick et al. 1977) supports the hypothesis that the island-like configurations of Peru's many isolated mountain ridges have provided conditions of reduced competition within which relict populations could persist and differentiate. The new *Heliangelus* described here is only 1 such example. Exploration of these ridges continues to produce new forms with remarkable frequency (see O'Neill and Graves 1977).

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VOCAL REPERTOIRE AND ITS POSSIBLE EVOLUTION IN THE BLACK AND BLUE JAYS (*CISSILOPHA*)

JOHN WILLIAM HARDY

The 4 allopatric Middle American jays of the taxon *Cissilopha*, which I treat as a subgenus of *Cyanocorax* (Hardy 1969), are communally social year round (Hardy 1976, Raitt and Hardy 1976). The species are the Yucatan Jay (*C. yucatanica*), Bushy-crested Jay (*C. melanocyanea*), San Blas Jay (*C. sanblasiana*, with 2 distinct races, see Hardy and Raitt 1977), and the Beechey Jay (*C. beecheii*). Their displays as a group are distinctive although not very elaborate (Hardy 1974b). Their vocal repertoires superficially seem small, as short-term experiences in the wild usually allow the observer to hear only 1 or 2 call types and these mainly from excited groups. Each form has a more extensive vocabulary.

In this paper I describe the known vocalizations, assign them to behavioral or motivational contexts, show some context patterns in tabular form, and speculate on the possible nature of evolution of vocabulary in the group.

METHODS

As described in detail elsewhere (Hardy 1973, 1974a, b, 1976; Raitt and Hardy 1976) all these jays were studied in the wild and in captivity. Recordings were analyzed on a Kay Electric Company Sona-Graph, Model 7029A, for sonograms (all wide band) presented here. All recordings or exact copies of them are deposited in the Bioacoustic Archive of the Florida State Museum's Department of Natural Sciences. The 4 tables showing context and pattern of vocalizations are based entirely upon tape recorded sequences in the Archive. In the discussion of the vocalizations, I have used my aural experience in many additional field hours with the birds in an attempt to compensate for the bias inherent in a quantitative approach to repertoires based only on recorded sound specimens.

RESULTS

In this section each species' vocalizations are treated separately.

Yucatan Jay.—The Yucatan Jay apparently has the largest active vocabulary of the 4 species. That is, more of its known vocalizations can be heard in the normal course of events while the birds are studied in the breeding season (Table 1). A description of the vocabulary of this species provides a basis for comparative consideration of the sounds of the remaining 3 species.

My 1969 paper showed narrow band sonograms of vocalizations of *C. yucatanica*, and Hardy (1974a) illustrated calls including one shown in both papers. These and several other calls are illustrated in Figs. 1 and 2. I have revised the phonetic interpretation of 2 vocalizations (from *clok!* to *clank!* and from *crook* to *chook*); 1 vocalization in Fig. 1, line 5, H of Hardy

TABLE 1

PATTERNS AND CONTEXTS OF YUCATAN JAY VOCALIZATIONS

	Contexts 1–9 (Contexts 3, 5, 6, treated only in footnotes)											
	1		2		4		7		8		9	
Call type	N	%	N	%	N	%	N	%	N	%	N	%
Chatter	32	27.8	5	7.1	6	10.7	10	58.8	7	53.8	10	19.2
"Fear"							1	5.7				
Rattle	2	1.7									1	1.9
Cauh	2	1.7							6	46.2		
Chook chook	1	0.8			50	89.3					1	1.9
Pump-handle	1	0.8	8	11.4			2	11.8				
Guttural tin-horn piping	1	0.8										
Clear tin-horn piping	5	4.3										
Metallic yelp	7	5.6										
Foggy bell	19	16.5										
Clanks	21	18.3	51	72.8							29	55.8
Peeps	24	20.9	6	8.6			4	23.5			1	1.9
Peer											6	11.5
Wooh!											2	3.8
Coo-caa											2	3.8
Total calls	115		70		56		17		13		52	
Total time (sec)	1864		95		180		130		38		260	

[1] Group of 6–10 birds, attending army ant swarm, April, dry season. Seven recorded sequences at 1 sitting. Jays 2–10 m away.

[2] Same as 1, except July, wet season, with juveniles in group. Birds along roadside.

[3] Group of 10–15 birds mobbing fox on ground, April. Chatter only. 45 sec (N = 4, % = 100).

[4] Two birds foraging in brushy field along forest edge, often out of sight of each other, mostly unaware of observer, April. Sequence twice interrupted briefly.

[5] General bird-human encounter. No specific circumstances, July. Continuous chatter only. 35 sec in single burst (% = 100).

[6] Same as 5, but at nest-site. Observer immobile, July. Chatter only. 120 sec, 85 and 20 sec bursts.

[7] Same as 6, but observer trying to examine nest contents with mirror on pole, July.

[8] Group with fledglings. Humans searching for young, July.

[9] Bird-human encounter, group having ¾-grown juveniles in it, July.

(1969) is now considered to be a variant of the *clank!* call. *Sotto voce* song is not illustrated here.

Three related loud harsh calls are spectrographically noisy. All were used in the general context of alarm. The staccato, rapid-fire, harsh "chatter" (Fig. 1A) was the call most frequently heard in the wild and is the Yucatan Jay's most obvious species-specific vocalization. "Chatter" is a social-alarm call. Birds chattered when discovering potential danger on the ground or in a tree. A fox, human, or squirrel readily stimulated such calling. A jay's

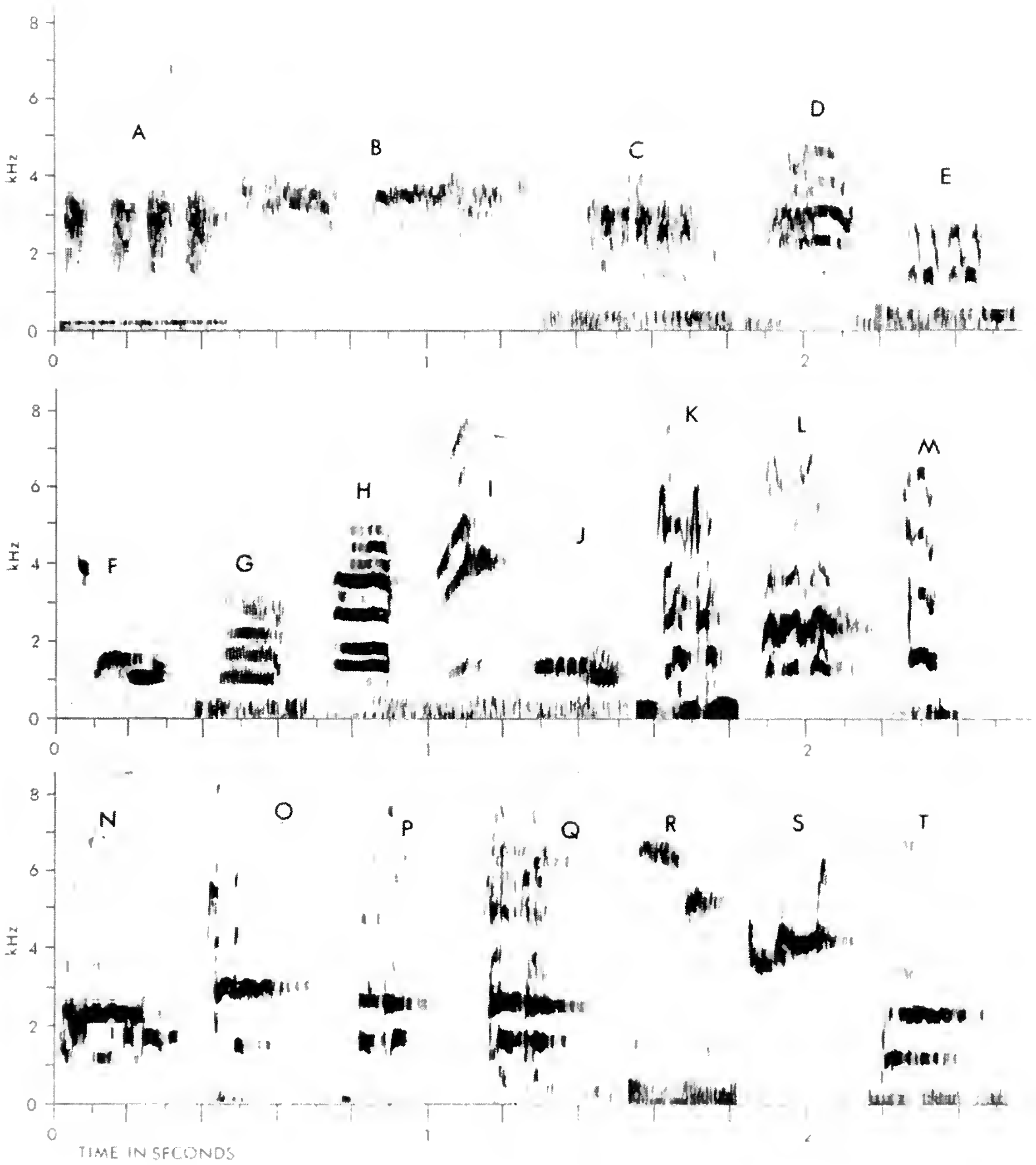

FIG. 1. Sonograms of vocal specimens of Yucatan Jays. Specimens are designated by their Moore Laboratory of Zoology (MLZ) master tape catalog numbers, Florida State Museum (FSM) master tape cut and species cut numbers, and recording dates. All recordings by J. W. Hardy, at Zoh Laguna, Campeche, Mexico, except B and T, recorded at Moore Laboratory of Zoology. (A) Chatter (MLZ 29, FSM 47-10-8, 9 April 1968); (B) "fear" call (MLZ 42, FSM 55-2-11, 23 May 1969); (C) rattle (MLZ 30, FSM 48-2-10, 13 April 1968); (D) begging *caah* (MLZ 42, FSM 55-2-11, 23 May 1969); (E) *chook chook* (MLZ 31, FSM 48-16-10, 14 April 1968); (F) "pump-handle" (MLZ 29, FSM 47-10-8, 19 April 1968); (G) guttural "tin-horn piping" call; (H) clear "tin-horn piping" call; (I) metallic "yelp;" (J) "foggy bell;" (K–Q) variants of resonant *clank* or *clank-clank*; (R,S) *tsi-peep, p-pee-eep* (G–S, all MLZ 29, FSM 47-10-8, 9 April 1968); (T) *peyook* (MLZ 44, FSM 55, no cut assigned, no date given).

chattering alerted other jays, which also usually gave the call and/or rapidly moved to the scene of the potential danger. When we played recordings of chatter it regularly caused jays to approach us. In fact, we used this method in censusing the population. "Chatter" occurred in all 9 contexts shown in Table 1. In context 1, however, it was not given by birds actively attending the army ant swarm but only by arriving birds that discovered us. After "chatter" has been used to notify of danger, a convention of jays uses the same vocalization in mobbing. Cadence varied from regular to the achievement of a rolling effect; rate of utterance increased with level of stimulation, grading, in 1 kind of circumstance, into the "fear" call (Fig. 1B). This call is thinner and less structured. The "fear" call was typically evoked by a predator or human touching the eggs or young in the nest (Table 1, context 7), and was accompanied by pecking or threats of attack. "Chatter" also grades into the rapid "rattle" (Fig. 1C) that resembles "chatter" in internal structure and tonal spectrum, but is more diffuse with a less staccato quality or a less steep wave front to the successive call components. This feature of the rapid "rattle" plus the approximately 2 kHz lower frequency limit are ascribed by Marler (1956) to effective avian-predator alarm calls. I had more difficulty locating birds giving this call, thus it may give a measure of protection to the caller while giving a warning signal to its cohorts. I heard this call given at Zoh Laguna, Campeche, Mexico, when a Collared Forest Falcon (*Micrastur semitorquatus*) flew fast and low over a flock of Yucatan Jays foraging at an army ant swarm (as in Table 1, context 1). I also heard it given twice by my captive flock when a Red-tailed Hawk (*Buteo jamaicensis*) soared overhead.

The begging *caah* (Fig. 1D), such as that given by the adult ♀ on the nest, was accompanied by slight wing fluttering and gaping; response by other birds was to feed the begging bird (Table 1, contexts 1, 8). In late incubation such calling was regular and probably encouraged increased visitation to the nest by other flock members and their readiness to bring food. More intense versions of this call have a squawk quality. Young birds often gave such begging "squawks" when feeders approached. These "squawks" (not illustrated) seemed to stimulate such approach.

The complex *chook chook* (Fig. 1E) was the second most often heard call, although Table 1, based on tape sequences only, does not reflect this. It is composed of 2 or 3 figures and was given as a social contact call by birds foraging or moving slowly in a loose group. At such times the birds were not so close together as to be regularly in visual contact. Each then gave occasional *chook* calls as it moved and fed. When I saw birds giving these calls, they were busily intent on feeding and unaware of our presence (Table 1, context 4). Playback of *chook* calls evoked no visible response.

The "pump-handle" (Fig. 1F), is a simple, mellow, low-pitched call, which sounded to the human ear as if composed of 2 parts, *pleeop.* Spectrographically 3 figures are revealed. I recorded and heard it 3 times (Table 1, contexts 1, 2, 7). This type of call is widespread in the "Ornate Line" of New World jays (Hardy 1969) that includes *Cyanocitta* and *Cyanocorax* (*sensu lato*). The context in which I heard it is discussed below; this call suggests a low intensity conflict of motivations.

Resonant calls are the guttural and clear "tinhorn piping" calls, the metallic "yelp," the "foggy bell," and the *clank* or *clank-clank* calls, of which there are many variants. These are shown in Fig. 1G–Q. I (Hardy 1974a) have heard the piping calls, "yelp," and "foggy bell" only from birds attending an army ant swarm (Table 1, context 1) and speculated that they might be specialized for that context. It seems possible (though my experience does not support the view) that any situation where excitement and marked motivational conflict occur could evoke these calls, as well as the "pump-handle" that was also heard at an army ant swarm. Such motivational conflict is otherwise characterized by sleeked plumage, quick jerky movements, tail flicking, slight bobbing, and sudden, short back-and-forth flights, as when taking insects from an army ant swarm. Resonant calls were usually given abruptly by individuals that were otherwise almost silent.

High-pitched, pure tonelike calls sound like intensive "peep" notes, but, as Fig. 1R and S shows, they are structurally more complex, with either 2 or 3 components. The first may be written phonetically as *tsi-peep* and the second as *p-pee-eep.* They were noted in context with the resonant calls discussed above (Table 1, contexts 1, 2) as well as in other situations in which motivational conflict seemed likely (Table 1, contexts 7, 9). The 2 forms of "peep" notes are not distinguished from each other in Table 1. One sonogram (not illustrated) showed a *clank* followed quickly by a *p-pee-eep*! We noted that 1 recorded example of *tsi-peep* was accompanied by a deep bobbing motion and an aspect of intense alertness. The food discovery call (Fig. 1T) may be written *peyook.* When the captive flock or one of its members discovered a new food supply, they gave this call. I did not hear this call in the wild.

Fig. 2A, B, C shows sonograms of 3 calls heard and recorded only once (Table 1, context 9) in which a group of jays were tending nearly grown juveniles. On this occasion the jays gave social alarm "chatter" calls at me, and then when I did not approach, they uttered the resonant *clank-clank* (Fig. 1K–Q) throughout the rest of the recording period. Interspersed among these calls were 2 each of the *wooh!* calls and the *coo-caa* and 6 of the *peer* calls (Fig. 2A–C), given in a context of apparent motivational conflict.

Fig. 2D is a sonogram of the location call of a young fledgling. It is not shown in the tabulation of contexts. The structure of such calls is poorly

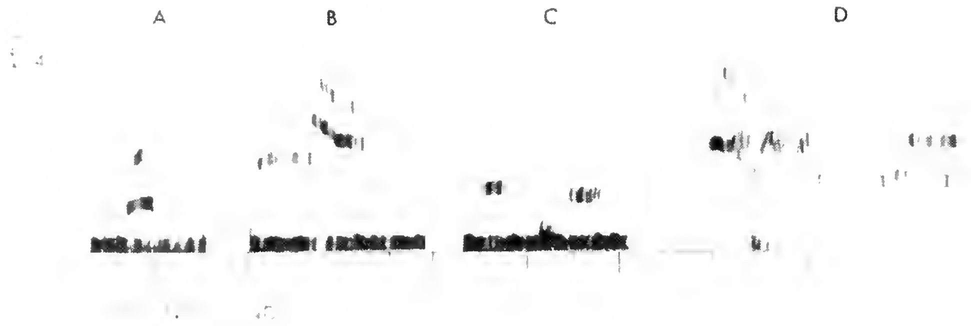

FIG. 2. Sonograms of additional vocal specimens of Yucatan Jays. See Fig. 1 for catalog number code. (A) *Wooh*; (B) *peer*; (C) *coo-caa* (A–C, all FSM 5-5-3, 12 July 1973); (D) fledgling location call (FSM 9-5-4, 23 July 1973).

defined and sounds to the ear like developmental stages of the "chatter" call. Fledglings of species treated below have aurally similar calls but these have escaped my recording.

Sotto voce song is rare in this species. I have not heard it in free birds but did so occasionally in captives. The song and associated display is described under the San Blas and Bushy-crested jays, which regularly perform them. Rarity in the present species may be associated with dark irides and the consequent lack of the constricted pupil display (Hardy 1974b).

San Blas Jays.—*C. sanblasiana* has 2 well-differentiated races, the nominate form (Southern San Blas Jay) and *nelsoni* (Nelson San Blas Jay), not in geographic contact at present and having social/alarm calls distinguishable from one another (Hardy and Raitt 1977). The extreme of differentiation of these calls is illustrated in Fig. 3A and B. In comparison to the "chatter" call of the Yucatan Jay, those of the San Blas Jays are nasal and less staccato. There is considerable variation in pitch and cadence in the utterance in different individual birds. Some are consistently shrill and very rapid (Fig. 3B) and others softer and sustained, *cacaah*, with an oft-repeated stereotyped pattern (Fig. 3C). As in *C. yucatanica* "chatter" is the most frequently heard call included in almost any context (Table 2).

A sustained, soft, begging *caah* (Fig. 3D) is given by incubating or brooding ♀♀ and also by food-begging juveniles (Table 2, contexts 2, 7). This is comparable to the Yucatan Jay's begging call (Fig. 1D). During extreme stimulation, as when an observer attempts to examine the nest, the chatter call grades into a "fear" call (Fig. 3F, Table 2, contexts 5, 6).

C. s. sanblasiana has an overhead predator "rattle" call (Fig. 3E, Table 2, context 9), but in our study area, hawks were virtually absent and thus the call rare. I have tape recorded it only once, when a group of 3 or 4 jays responded to a Grey Hawk (*Buteo nitidus*) flying overhead at tree top height.

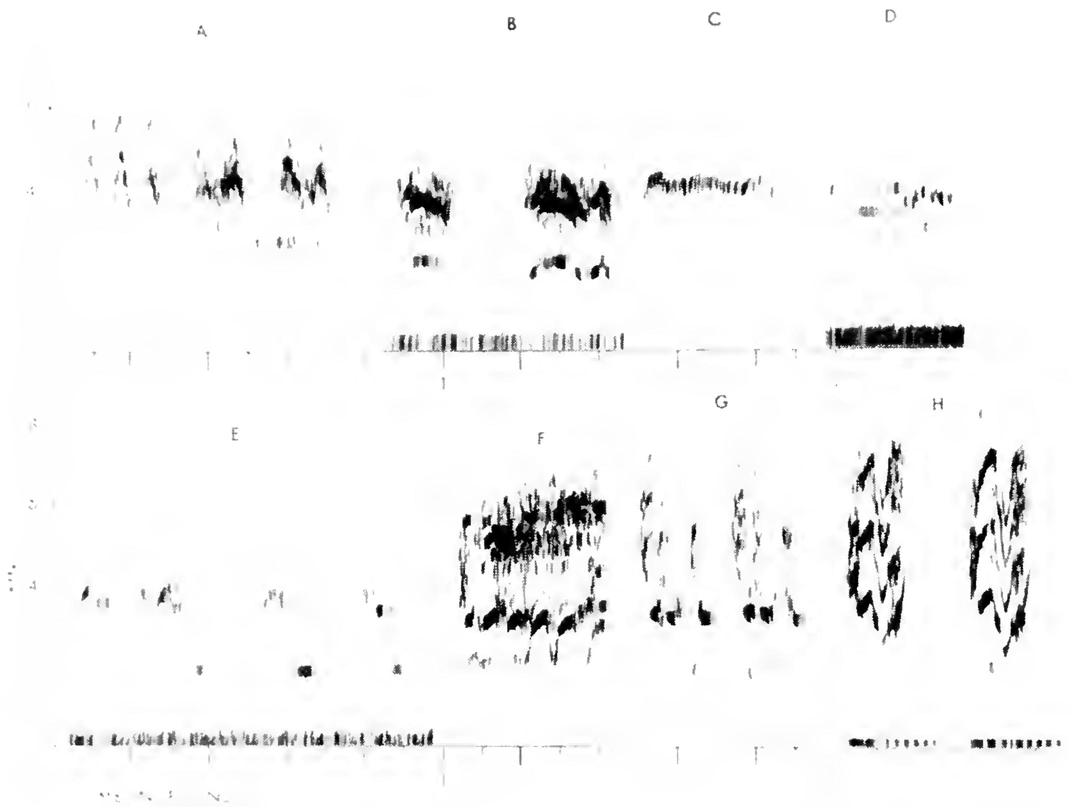

FIG. 3. Sonograms of vocal specimens of *Cyanocorax sanblasiana*. See Fig. 1 for catalog reference numbers code. *Cyanocorax s. nelsoni*: (A) "chatter" (MLZ 39, FSM 53-24-7, 26 June 1970); *C. s. sanblasiana*: (B–D) "chatter" (more sustained figures) (FSM 29-1-1, 27 June 1975); (C) social alarm call of 1 bird showing distinctive constant variant form from most frequently given form (FSM 161-19-10, 24 June 1976); (D) sustained *caah* (FSM 29-1-1, 27 June 1974); (E) "rattle" (FSM 324-4-15, 6 July 1977); (F) "fear" call (FSM 162-4-11, 7 July 1976); *C. s. nelsoni*: (G) *chank chank* contact call (MLZ 38, FSM 53-20-6, 18 June 1970); *C. s. sanblasiana*: (H) resonant *clank-clank!* (FSM 161-20-11, 24 June 1976).

Fig. 3G shows the 2-note counterpart of the *chook chook* calls of the Yucatan Jay (Fig. 1E). Both races of San Blas Jay utter this 2-note counterpart, a more resonant *chank chank* sounding call. Its function seems to be the same as in the Yucatan Jay—a social contact call given by birds that cannot see one another (Table 2, context 1). In situations where high levels of motivational conflict would be predicted, a complex, resonant call (Fig. 3H) similar to the Yucatan Jay's metallic "yelp" or to its resonant *clank!* is given by individuals of the nominate race (Southern San Blas Jay). It is rarely given; we heard it uttered by an adult excitedly watching us remove a jay from a mist net, and also from parent birds when we disturbed nests while viewing their contents (Table 2, contexts 5, 6).

The *sotto voce* song is part of a display in which the pupils are constricted

TABLE 2

PATTERNS AND CONTEXTS OF SAN BLAS JAY VOCALIZATIONS

	Contexts 1–9 (Contexts 3, 4, 8 treated only in footnotes)											
	1		2		5		6		7		9	
Call type	N	%	N	%	N	%	N	%	N	%	N	%
Chatter/caw	18	85.7	24	88.8	27	17.0	11	57.9	78	91.8	4	67.7
Sustained caw			3	11.2					6	7.1		
Begging (juvenile)									1	1.0		
Rattle											1	33.3
"Fear"					120	75.5	3	15.8				
Chank chank	4	14.3										
Clank-clank!					12	7.5	5	26.3			1	33.3
Total calls	21		27		159		19		85		6	
Total time (sec)	120		155		90		90		190		15	

[1] Immediately after a period of mobbing of unseen animal. Near nest, June.
[2] Foraging bird. Chattered at observer, then gave 4 two-note contact calls, June.
[3] Adult male near nest, observer close by, July. Chatter/caw only. 35 sec (N = 35, % = 100).
[4] Two or 3 birds mobbing unseen animal, near nest, June. Chatter/caw only. 35 sec (N = 35, % = 100).
[5] Two observers operating nets near nest with young, catching jays and marking them, also examining nest contents, July.
[6] Observers near nest with eggs or young, July.
[7] Loose group feeding half-grown juveniles or fledglings. Observers in sight, June.
[8] Same as 7. Chatter/caw only. 12 sec (N = 12, % = 100).
[9] Small group of foraging birds. Grey Hawk sails overhead.

(see Hardy 1974b). The song is complex and melodious and occurs in situations where conflict of motivation might be expected, as in courtship, but also it can be evoked by the suddenly detected presence of a human (or other "predator?"). Such song in another species is illustrated in Hardy (1969).

Bushy-crested Jay.—This jay has a repertoire similar to that in the San Blas Jay. The harsh loud social alarm "caw" (Fig. 4A) is neither staccato nor nasal as in San Blas or Yucatan jays. Instead, it is intermediate to these and the sustained cawing of *C. beecheii* (Fig. 4E). To my ear and by sonogram the sound more closely resembles the social alarm call of the Beechey Jay. Context is like that of social alarm calls of the other species (Table 3, contexts 1, 2, 4, 5). I have not heard an overhead predator "rattle" or the rapid "fear" call in this species.

A soft begging "caw" in *C. melanocyanea* is shown in Fig. 4B. It is comparable to those already described, and is given in the same circumstances by brooding or incubating females (Table 3, contexts 3, 4). The short "caw"

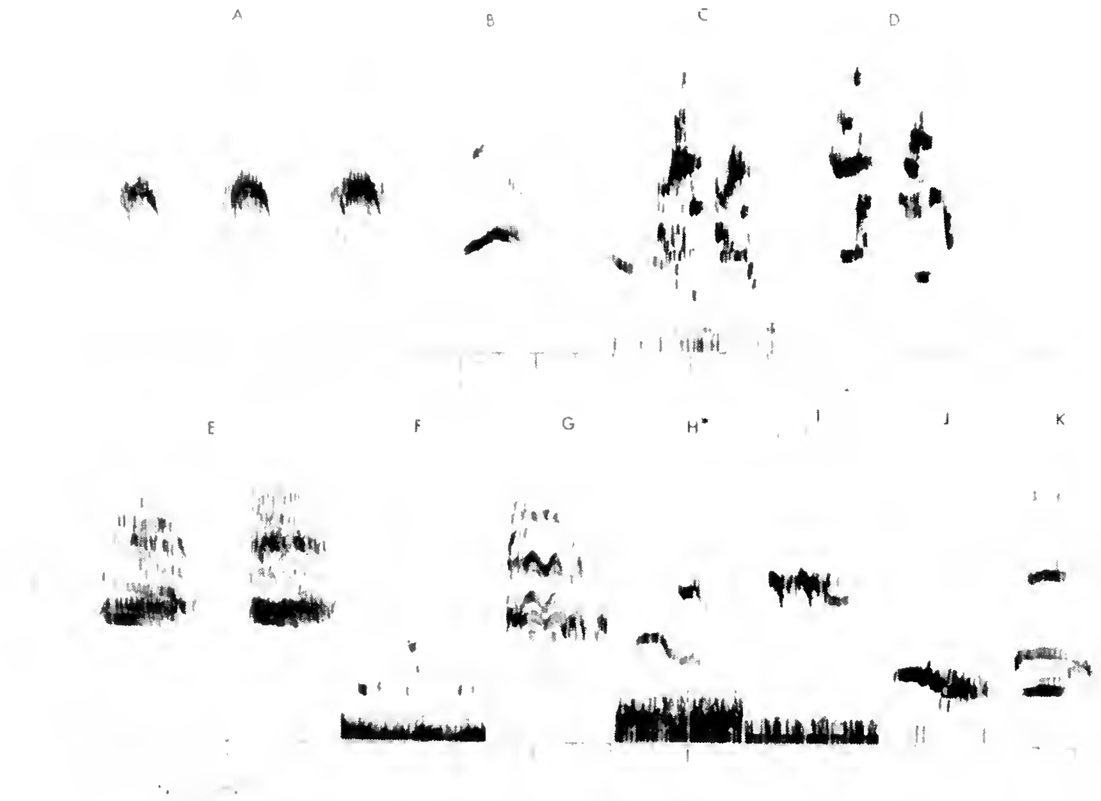

FIG. 4. *C. melanocyanea*, *C. beecheii*, *Corvus sinaloae*. *C. melanocyanea*: (A) social alarm "caw" (MLZ 34, FSM 50-7-1, 14 June 1976); (B) begging "caw" of ♀ on nest (MLZ 35, FSM 51-12-4, 19 June 1969); (C) *chank chank* (MLZ 35, FSM 51-12-4, 27 June 1969); (D) resonant *chank chank* of captive bird (MLZ 40, FSM 54-4-9, 24 March 1971); *C. beecheii*: (E) social alarm "caw" (FSM 160-3-3, 14 June 1976); (F) *clok clok clok* (FSM 327-15-8, 6 June 1977); (G) "quavering caw" (FSM 32-11-2, 24 June 1974); (H*) "crying" call (FSM 65-11-4, 3 December 1975); (I) intense *peep!* (same data as H); (J) *pook* (MLZ 44, FSM 55, no cut assigned, no date given); *Corvus sinaloae*: (K) social call *weer* (FSM 160-7-1, 14 June 1976).

of juveniles (not illustrated) combines elements of begging and location (Table 3, contexts 2, 5, 7).

The basic 2-note contact call, *chank chank*, of the Bushy-crested Jay (Fig. 4C) is similar to that of the San Blas Jay, being more resonant than that of the Yucatan Jay. In my experience, this call is rarely given. I recorded it twice in the wild—I believe the only times I heard it in a 3-week study (Table 3, contexts 2, 5). I heard an often given variant of the call from a captive bird (Fig. 4D).

Sotto voce song is common in this species. As in the San Blas and Beechey jays it is associated with a display in which the pupils are constricted (Hardy 1974b). As in other jays that give this song, it is barely audible a few m

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* Frequency scale on 4, H is 40–4000 Hz.

TABLE 3

PATTERNS AND CONTEXTS OF BUSHY-CRESTED JAY VOCALIZATIONS

	Contexts 1–7 (Contexts 1, 3, 6, 7 treated only in footnotes)					
	2		4		5	
Call type	N	%	N	%	N	%
Caw	1	1.4	2	50.0	7	77.6
Begging caw			2	50.0		
Short caws (juveniles)	63	88.7			1	11.2
Chank chank	7	9.9			1	11.2
Total calls	71		4		9	
Total time (sec)	290		25		30	

[1] Loose group of 10–15 adults with full-grown juveniles. Response to human squeaking sounds, June. Caw only; 135 sec (N = 8, % = 100).

[2] Same as 1, June.

[3] Three or 4 birds near nest, including 2 juveniles, June. Begging caw only; 61 sec (N = 5, % = 100).

[4] Same as 3, June.

[5] Full-grown juvenile perched near nest with young. Adults coming and going, feeding young, June.

[6] Begging female on nest with 3 eggs; male feeds her and she leaves. Begging caw only; 70 sec (N = 16, % = 100).

[7] Group of 3 or 4 almost grown juveniles moving in understory along trail in forest, giving short begging and cawing calls. Short calls (of juveniles only); 230 sec (N = 37, % = 100).

away, is complex and melodious, and is given in courtship situations as well as by isolated birds. Sudden sight of me by captive birds often evoked such song from 1 individual. It may be associated with conflict of motivation, as in courtship.

Beechey Jay.—*C. beecheii* seldom utter any sounds except harsh "cawing" sounds (Fig. 4E). These are variable in cadence, amplitude, and configuration, differing little if any from bird to bird but more with respect to context and level of apparent motivation. The call in a social alarm context (as figured) is very *Corvus*-like. This is intriguing, since the small Sinaloa Crow (*Corvus sinaloae*) with which the jay is syntopic, has a very uncrow-like call *weer* (Fig. 4K) very much like that found in several *Cyanocorax* species (see Hardy 1969). The harshness of the call in the Beechey Jay is typical for *Cissilopha*. Therefore, if character displacement (Brown and Wilson 1956) has operated in the area of sympatry between Sinaloa Crows and Beechey Jays, it seems it is the crows' calls that have been altered. Further evidence for this belief is the fact that the social alarm calls of all other North American crows are harsh. This includes the call of the very similar Tamaulipas Crow (*Corvus imparatus*), which Davis (1972) describes as "a frog-like *gurrr*." Davis' apt description of the call of the Sinaloa Crow

TABLE 4
CONTEXTS AND PATTERNS OF BEECHEY JAY VOCALIZATIONS

	Contexts 1–3					
	1		2		3	
Call type	N	%	N	%	N	%
Caw	43	77.0			19	61.3
Quavering caw	10	23.0				
Clok clok clok					12	38.7
Plaintive cry			3	42.9		
Two-note peep!			4	57.1		
Total calls	53		7		31	
Total time (sec)	225		36		120	

[1] Adult pair at nest, observer at base of nest tree.
[2] Flock of 6 to 8 birds, moving and foraging in forest, aware of stalking observer, out of sight, December.
[3] Three observers at nest, eggs newly missing, adult pair owners of nest ca. 100 m distant, 1 calling caw and the other the *clok clok clok* call.

also lends support to the theory presented here: "A relatively shrill ceow . . . very much like that of the Brown Jay of e. Mexico."

Selective advantage of character displacement and resulting dissimilarity of the social alarm calls of the jay and the crow seem clear: the vocalizations in both cases have only intraspecific significance, signaling members of the same species to convene. Dissimilarity avoids confusion of the signals.

A distinct variant of the social alarm call is the "quavering caw" (Fig. 4G) comparable to the "fear" call of the other species and given under similar circumstances (Table 4, context 1). *Sotto voce* song is common in the specific context of courtship in this species, again associated with a display as described in Hardy (1974b). The song as in the other species is complex and melodious.

Other calls of the Beechey Jay are so rarely given that I have thus far recorded only 3 in the wild and each of these only once. The contact call (and sharply resonant variants) is usually of 2-figure structure and resembles those of the other species. The basic version (Fig. 4F, Table 4, context 3) is soft with a marimba-like quality (*clok clok clok*) most like that of the Yucatan Jay (Fig. 1S) but of similar character to my ear. The behavioral and motivational context of these 2 calls are not known.

My captive Beechey Jays gave a food discovery or expectancy call (Fig. 4J) that may be described as a mellow *pook* sound. It was given in the same context as the somewhat higher-pitched *peyook* (Fig. 1T) of the captive Yucatan Jay nearby, and like that note, only when food was being placed in the aviary.

DISCUSSION

Only the social alarm call ("chatter" and "caw") is a really common vocalization, though it has many variations, in all of these jays. In the Yucatan Jay the contact call is infrequently uttered in the wild, yet is heard daily. In the Beechey Jay the call is so rarely uttered that, as previously mentioned, I only once tape-recorded it. If one is in the field for 4 h a day from approximately 06:00–10:00 throughout the breeding season I estimate that he would hear the call an average of less than once a day. Begging calls are to be heard from incubating or brooding females, but not all such birds give these calls regularly, and they seem to be restricted to that context.

Only in the Yucatan Jay are other calls such a frequent part of the repertoire that one can expect to hear and record them in a period of a few days' time. With the exception of the calls so far heard only in the context of army ant swarm attendance (Table 1, context 1) and from jays tending juveniles when the observer was nearby (Table 1, context 9), the Yucatan Jay's actual repertoire is also its active repertoire. Under circumstances of stress, where motivational conflict can be predicted, this jay displays an unusual variety of other calls compared to its close relatives. In my personal experience, the repertoire, as with Magpie-jays (*C. formosa*) and Blue Jays (*C. cristata*), seems to be expandable at a given moment by individual invention of call types. The Collared Jay (*Aphelocoma viridicyana*) is another tropical latitude jay that has a bewildering number of calls, some of which I naively called non-jay-like calls (Hardy 1967) and tried to relate to habitat density and association with other species in mixed flocks. Certainly the Yucatan Jay has a visually more restrictive habitat than that of its close relatives treated in this paper; thus, perhaps the large repertoire bears some relationship to habitat character.

Highly unusual circumstances such as those already described seem also to evoke greater variety of sounds in the Bushy-crested and San Blas jays, while in the Beechey Jay no situation that one can easily contrive, such as examining the nest contents, can be depended upon to evoke other than the harsh cawing sound: the rare components of the vocabulary seem to be given almost at random, although this is unlikely to be the case.

Elsewhere (Hardy 1969) I have discussed how I believe the main pathway of evolution of plumage pattern and ornamentation in the New World jays of the Ornate Line has proceeded from complex to relatively simple. Thus, I regard species such as the elaborately and boldly plumaged Tufted Jay (*Cyanocorax dickeyi*) and Plush-crested Jay (*C. chrysops*) to be phenotypically least derived from the ancestor of this group. Intermediate forms include the Cayenne Jay (*C. cayanus*) and Black-chested Jay (*C. affinis*). Four of the phenotypically highly derived forms are the subjects of this paper; others are the Brown Jay (*C. morio*), Azure Jay (*C. caeruleus*) and Purplish Jay (*C. cyanomelas*).

The evidence in phenotypes and ontogeny of plumage and soft part coloration (Hardy 1973) is that the "simplification" process has not been a simple one. Thus in the Black and Blue jays (subgenus *Cissilopha*) different disappearing ancestral traits are to be found in different species. The Yucatan Jay reveals the white-tipped tail in the first year stage; the Bushy-crested Jay retains the feature of black chest divided from paler abdomen, and the San Blas Jay has the prominent tufted fronto-nasal crest, well-developed in the juvenile, and gradually less so in yearling, 2-year-old and adult stages of the nominate form and virtually absent after the yearling stage in the race *nelsoni*.

It is my judgment that something similar to this simplification process is occurring in vocal repertoire. The Yucatan Jay retains the most elaborate actively-used vocabulary, while the other species seem to have simpler active ones, with some vocalizations being used infrequently in certain unusual contexts that would be expected to evoke fear and conflict of motivation or, rarely, in seemingly haphazard form and context.

I believe that the small size of the active vocabulary in the Beechey Jay is related to its lesser degree of sociality (Raitt and Hardy 1979). The size of this species' social breeding units is smaller by at least half that in the other species.

There is general support for this hypothesis in another New World species the Dwarf Jay (*Aphelocoma nana*) (Hardy 1971), which to my knowledge is the least social of all New World jays. Breeding pairs in the nesting season are solitary and essentially nonvocal. They can usually be provoked to call only by extreme measures, such as tampering with the nest. Ordinarily there is only 1 vocalization, the doubly inflected *shreéup!* When the nest is touched, the birds utter the harsh rasping rage call, but otherwise only variants of the *shreéup!* are to be heard. Nonbreeding flocks are small and slightly more vocal, but also utter only variations of the *shreéup!* call.

SUMMARY

The 4 species discussed are the closely related allopatric Yucatan, Bushy-crested, San Blas and Beechey jays of the genus *Cyanocorax*, usually grouped in the taxon *Cissilopha* (here considered to be a subgenus). The Yucatan Jay has the largest vocal repertoire—24 call types are illustrated and discussed—about ⅕ of which is active, that is, employed frequently in "everyday" situations in the breeding season. Harsh staccato chatter constitutes the social alarm call and is the commonest utterance. The 2-note call seemingly serves as a contact call between individuals of a group not within sight of each other. Other calls include distinctive variations of the 2-note, overhead predator call, fear call, and a variety of calls that along with the 2-note variants seem to be typical of motivational conflict associated with unusual contexts.

The San Blas Jay has 2 races that differ in 1 consistent way in vocalizations. The Southern San Blas Jay (nominate subspecies) has the social alarm call composed of simple regular nasal figures plus more complex sustained figures; the Nelson San Blas Jay utters only the simple figures. In the Southern San Blas Jay individuals may have consistently identifiable deliveries of the social alarm call. Besides a "fear" call and this call, others are 2 variants of the 2-note call.

The Bushy-crested Jay has a social alarm call that may be described as a short cawing figure, intermediate in length between the short calls of the above 2 species and that of the Beechey Jay. A begging call and 2 variants of the 2-note call are shown and discussed.

The Beechey Jay possesses the smallest active vocal repertoire. The only commonly heard call is a crow-like cawing without much interindividual variation but considerable variation in rate of delivery and cadence, depending on context. A distinct variant of this call is the "quavering caw" representing the "fear" call in this species. A contact call is seldom heard, and the soft cry and a 2-syllable peeping are rare. The former was heard mostly from birds that had just lost nests and eggs, presumably to predation. The Beechey Jay's very small vocabulary may be related to its smaller degree of sociality when compared to the other species considered in this study.

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ECOLOGY AND BEHAVIOR OF THE GALAPAGOS RAIL

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During his famous visit to the Galápagos Islands in 1835 Charles Darwin observed "great numbers of a very small water rail . . ." (Darwin 1896). This bird was *Laterallus spilonotus*, a species endemic to 7 islands of the Galápagos archipelago. Early studies of the Galápagos Rail (local name, "pachay") concentrated on taxonomy; despite the local abundance and relative tameness of this species, the information available on its ecology and behavior has been only anecdotal. We report here the results of a 10-month field study of this little-known bird.

METHODS AND STUDY AREAS

Ecological and behavioral data were gathered during approximately 150 person-days of field study (principally by ABF) between September 1973 and July 1974, on Santa Cruz Island, Galápagos, Ecuador. The 2 main study areas were in the highland regions. The Media Luna site (elevation 600 m) was in the vegetational zone of *Miconia robinsoniana*, a 1–3 m endemic shrub (zone nomenclature follows Wiggins and Porter 1971). This site included dense shrub areas with fern undergrowth, and open sedge–fern meadows. The Puntudo site (elevation 730 m) was in the open fern–sedge zone near the island summit.

The climate in the Galápagos Islands is biseasonal, with great variability among years. In the highlands the "hot season" (ca. January through May) is generally hot and sunny with sporadic heavy rains. The cool season (locally termed the "garúa season") extends from about June through December; day-long rain, drizzle, and fog are common.

Chicks were captured by hand or with a net; for larger birds the only effective method was to use a chicken wire box-trap propped up on 1 side. All captured rails were color-banded, and the following data recorded: weight (± 1 g); length of exposed culmen, middle toe with claw, and tarsus (± 0.1 mm); eye and bill color; and condition of plumage. Gut contents were aspirated from 6 individuals, and fecal samples were collected when located in the field.

Galápagos Rails were exceptionally tame and could be followed by an investigator crawling on hands and knees. Movements of individuals were mapped by triangulating marked locations of sightings. Rail calls were recorded on a portable cassette tape recorder and subsequently transferred to reel-to-reel tape. Sound spectrograms were made with a Kay Elemetrics Missile Data Reduction Spectrograph (and a Uher 4200 tape recorder), using a 200 cps wide band filter. Playbacks of these calls (on the original cassettes) were used to observe reactions of rails and Short-eared Owls (*Asio flammeus*).

ECOLOGY

Distribution and habitat.—The Galápagos Rail originally occurred in 2 habitat types: highland moist regions with dense ground cover, and coastal

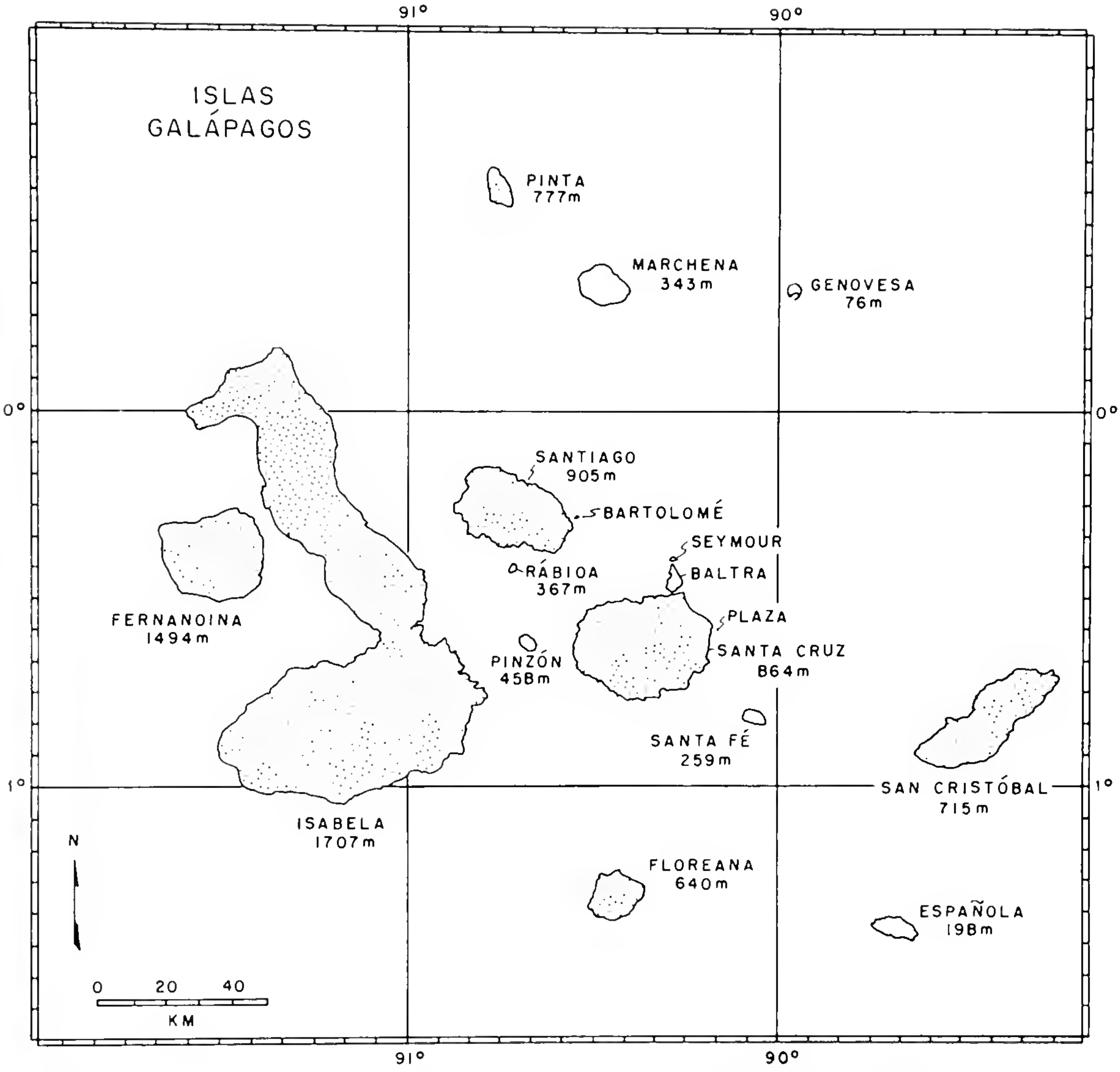

FIG. 1. Current island distribution (stippled) of *Laterallus spilonotus*. All islands higher than 500 m have rails.

mangrove zones (Salvin 1876, Rothschild and Hartert 1899, Snodgrass and Heller 1904, Gifford 1913). The species is no longer known from mangroves on any island. The reason for this habitat shift is unknown; Michael Harris (pers. comm.) has noted that exotic animals are unlikely to be a sufficient explanation, because rails seem to have disappeared from the mangroves of Fernandina, an island with no introduced predators or competitors.

L. spilonotus is now known only from those islands high enough to have an extensive moist region (Fig. 1). The rails' close association with the dense moist zone vegetation is illustrated by records from Pinta Island, where these birds were common in the fern belt of the highlands (Castro 1964, Charles Darwin Research Station 1968). Goats were introduced to Pinta in 1959; between 1968 and 1970 they moved into the moist region, clearing it

TABLE 1

BREEDING RECORDS FOR *LATERALLUS SPILONOTUS*, SANTA CRUZ ISLAND, GALÁPAGOS

Month	No. of nests with eggs or nestlings*	No. of broods with chicks**	No. of broods with juveniles
Jan–Feb	4	4	1
Mar–Apr	3	3	1
May–June	–	–	2
July–Aug	–	–	–
Sept–Oct	–	3	–
Nov–Dec	2	3	–

* 6 nests (Tui De Roy pers. comm.)

** 1 brood (Gil De Roy pers. comm.); 1 brood (Tui De Roy pers. comm.); 1 brood (Chapin 1930); 2 broods (Edinburgh Expedition 1968), both cited as "young" (chicks?); 1 brood ("small young") (Craig MacFarland pers. comm.); 1 brood (Henk van der Werff pers. comm.).

of all vegetation except trees and some shrubs (Weber 1971). During 2 visits to Pinta in 1970, no rails were seen or heard (Kramer and Black 1970). Beginning in late 1971 the Galápagos National Park Service instituted a goat-hunting program. With the consequent great reduction of goats on Pinta, the undergrowth has returned. Tjitte de Vries (pers. comm.) found rails "common" on the island summit during 2 visits in 1973–1974.

On Santa Cruz, we have seen and heard rails in the following zones (described in detail in Wiggins and Porter 1971): the *Scalesia* forest (north and south slopes); the shrubby *Miconia* zone; the fern–sedge zone around the summit: and the moist farming regions. During 60 days in the much drier Transition zone we observed no rails.

Reproduction.—The few nest and brood records from Santa Cruz (Table 1) are from the months of September through April. Additional evidence of reproduction is scarce. Amadon (in Lévêque 1964) collected 2 males with enlarged gonads on Santa Cruz in April 1930. Gifford (1913) noted "somewhat enlarged" gonads in specimens taken in November 1905 (Santa Cruz) and January 1906 (Santiago). He also recorded a female with a well-developed egg and 2 other birds with enlarged gonads, all taken in September 1906 on Pinta. In June 1974 we observed 1 pair of Santa Cruz rails apparently courting (bill fencing, mutual preening). More breeding records, correlated with seasonal conditions, are necessary to describe reproductive patterns adequately.

Three *L. spilonotus* nests that we examined were deep semi-domed cups with a side entrance. Made of herbaceous stems, they were built on the ground and covered by dense, low vegetation. This nest construction cor-

FIG. 2. Pair of Galápagos Rails at change-over during incubation (photograph by Tui De Roy).

responds closely to that described for the Black Rail (*Laterallus jamaicensis*) (Clark 1884, Bent 1926).

The eggs were beige, with red-brown and some gray speckles (0.3–1.0 mm) sprinkled over most of the surface, particularly at the wide end of the egg. Three eggs from 1 nest measured 29.1 × 22.2, 29.0 × 21.6, and 30.2 × 21.5 mm (measured with calipers). Five eggs from another nest measured (with a ruler and thus less accurately) 28 × 20, 25 × 20, 26 × 20, 25 × 19, and 26 × 19 mm.

Eggs of the other small rallid of Santa Cruz, the Paint-billed Crake (*Neocrex erythrops*), are similar in size and shape to those of *L. spilonotus*. Paint-billed Crake eggs are cream-colored and flecked with red-brown and gray spots, clustered at the large end. These spots are mostly 1–3 mm, but some are as big as 6 × 10 mm. Three eggs from the only *Neocrex* nest we found measured 32.6 × 23.7, 32.5 × 23.8, and 33.9 × 24.0 mm; the nest was a low open bowl with no dome or roof, quite different from a *Laterallus* nest.

We found 1 Galápagos Rail nest with 3 eggs on 19 November 1973. On 13 December there were 2 dry young and 1 egg, giving a minimum incubation period of 23–25 days. The third egg never hatched.

In January 1975 Tui De Roy (pers. comm.) observed a pair of *L. spilonotus* incubating. The pair exchanged duty on the average every 50 min during several hours of observation. Each change-over included several minutes of mutual preening, with both members sitting in the nest (Fig. 2). The foraging birds seemed to remain within 10–15 m of the nest.

Data for clutch and brood size are limited. Six clutches of 3 to 6 eggs and 3 groups of 2 to 4 chicks on the nest have been found (Tui De Roy, pers. comm.; our observations). We saw numerous broods, but in the dense vegetation it was often difficult to count the chicks accurately. Seven broods of 1 to 5 young ($\bar{x} = 3.6$) have been recorded (Gil De Roy, pers. comm.; our observations).

One banded adult was associated with 2 broods in 1 season. On 13 and 14 February 1974 this bird was seen with 5 chicks. Two chicks (weights 20, 24 g) were banded; on 9 March one of these was recaptured (it then weighed 36 g). On 19 March the same adult was seen with a brood of at least 3 obviously newly-hatched chicks (the 2 captured weighed 13 and 14 g).

Growth and development.—Fig. 3 depicts the changes with increasing body weight of several external characters (data from 26 Galápagos Rails, captured 31 times). There is a progressive change of iris color from black through brown and orange to crimson as these birds mature (a very similar progression in iris coloration has been illustrated in color by Rowley [1974] for the White-winged Chough [*Corcorax melanorhamphus*]). Bill coloration also changes through development. As in Black Rails (Walker 1941), the bill of very young Galápagos Rail chicks is completely white over the proximal half, and is black on the tip. The area of the white patch decreases with age, contracting from the sides and from below. Once rails weigh ca. 28 g, the white area is only a small spot halfway along the culmen; the bill is completely black for all birds over ca. 37 g. Plumage coloration also changes with size in Galápagos Rails. An increasing portion (up to ¾) of the back becomes fuscous, and the white spotting increases, spreading out over the body and wings.

Regressions of the length of the tarsus, exposed culmen, and middle toe (with claw) on body weight are given in Table 2. While the first 2 measurements increase linearly with body weight, the increase of the middle toe is logarithmic, showing much more rapid growth in earlier development.

Because we did not autopsy birds, we could not correlate external characters with reproductive state; therefore we divided the rails arbitrarily into 3 "age" groups, as indicated in Fig. 3. The few intermediate birds were classified according to bill coloration. Although we based these groupings solely on external morphology, we found distinct behavioral differences

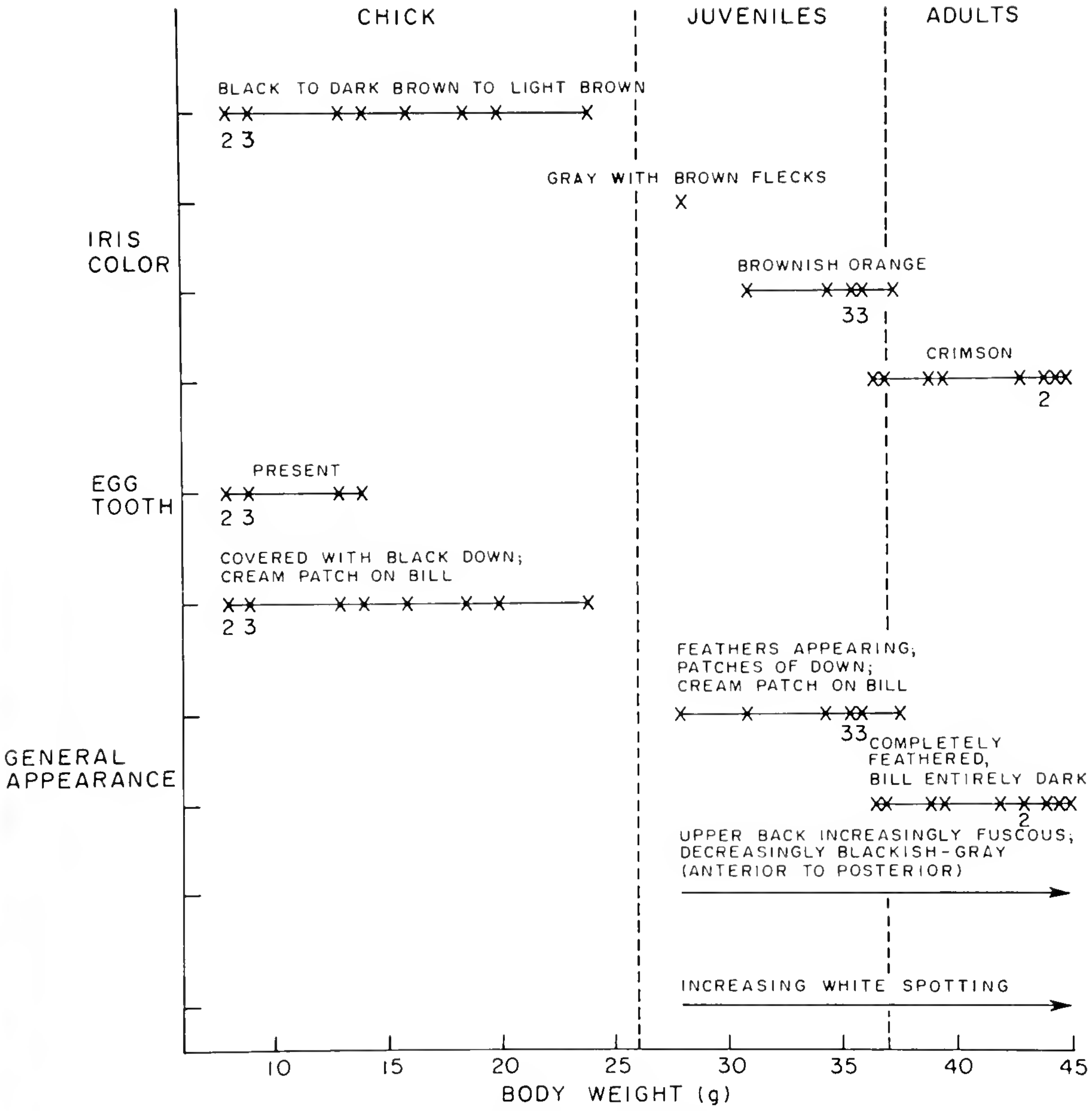

FIG. 3. Developmental changes of external characters in *L. spilonotus*. Subscripts indicate more than 1 individual.

between "juveniles" and "adults" (see Behavior). Non-"adult" birds were never seen exhibiting breeding behavior.

The data from all banded bird sightings and recaptures indicate that the transition from newly-hatched chick to "adult" requires 80–85 days. One individual, captured as a 9 g chick in December 1973, was observed with a mate and 4 young in December 1974 (Tui De Roy, pers. comm.).

Growth rates obtained from 4 recaptures were (with initial weight, final weight, and time between captures): 1.5 g/day (14–18.5 g, 3 days); 0.83 g/day (28–35.5 g, 9 days); 0.67 g/day (20–36 g, 24 days); 0.26 g/day (16–36.5 g, 78 days). From these data we infer that the growth rate is

TABLE 2

RELATIONSHIP OF 3 EXTERNAL MEASUREMENTS TO BODY WEIGHT(G) OF FREE-RANGING GALÁPAGOS RAILS

Dependent variable	N	Regression[1]	*r*
Tarsal length (mm)	26	$y = 12.88 + 0.27x$	.88***
Culmen length (mm)	29	$y = 4.46 + 0.28x$	.97***
Length of middle toe with claw (mm)	29	$y = 2.07 + 18.02\log_{10}x$	.82***

[1] Model II; calculations follow Sokal and Rohlf (1969:483).
*** $P < 0.001$.

initially rapid and then slows markedly as a bird reaches approximately 36 g.

Diet.—Field observations and analysis of 5 gut and 10 fecal samples indicate that Galápagos Rails eat primarily invertebrates. We identified the following food items (with total number of samples or observations in which the item occurred): dragonflies, 3; moths, 4; hemipterans, 7; ants, 1: spiders, 2; isopods, 1; amphipods, 1; snails, 1; and seeds, 4 (the ant and amphipod were very small and may have been incidental items). Fragments of arthropod exoskeleton were present in 4 of the gut samples and in all the fecal samples. Although we never observed rails eating plant materials, 1 stomach (from a Santiago juvenile) was approximately half-full of seeds from an unidentified solanaceous berry. Several seeds of *Miconia robinsoniana* were found in 1 gut sample. Another contained a few seeds of *Paspalum conjugatum* (Poaceae); these seeds are very adherent and may have been picked up in preening.

Predation.—Our single observation of a domestic dog killing a rail is the only record of predation on *L. spilonotus.* The Short-eared Owl, a known predator on the Black Rail (Huey 1926), commonly hunted in both our study sites. We observed individual owls flying toward and hovering over the area when they heard either taped rail calls or vocalizations of actual rails; however Abs et al. (1965) did not find remains of *L. spilonotus* in their study of Galápagos Short-eared Owl pellets.

Although black rats (*Rattus rattus*) were abundant at Media Luna (15/ha, Clark and Clark, pers. obs.), they appeared to have little or no effect on the rails, for *L. spilonotus* was common there. Rat predation on rail eggs may be prevented by the incubating adult's aggressive behavior towards intruders. While we were investigating 1 nest, the attending rail stayed in or very near the nest (Fig. 4a). It also actively defended the eggs, once by spreading its wings over the nest entrance (Fig. 4b), and once

FIG. 4a. Adult Galápagos Rail inside nest entrance.

by sharply pecking the investigator's hand as he reached toward the eggs. The 2 other nests observed, however, were not defended.

BEHAVIOR

We found Galápagos Rails active throughout the day (twice calling was also heard at night). Provided the observers remained still, they foraged calmly around us, often passing a few cm away without apparent disturbance. At times individuals circled and peered at us, seemingly very curious. Even when disturbed by sudden movements, birds sometimes returned after fleeing only a short distance.

Terrestrial locomotion.—Although Galápagos Rails occasionally fly and swim, they are basically ambulatory. When startled, they usually run

FIG. 4b. Same adult displaying above nest entrance.

rather than fly. Marked 9-g and 13-g chicks held their stubby wings out to the side as they ran. Movements were clumsy at this size, but the 13-g chicks were fast and not easy to capture. Older birds (⩾ 20 g) hold the wings close to the sides: the body and head are low to the ground as the rails run along a zig-zag pattern. The birds always seem to keep close to protective cover. When observed crossing open patches of ground, individuals always ran, either directly across or in rapid dashes with a pause of a few sec between each spurt.

Gifford (1913) observed that *L. spilonotus* on Santiago "traveled through little runways in the grass." In our Puntudo study area, such small beaten-down trails were very numerous under large patches of bracken (*Pteridium aquilinum*) and were usually strewn with droppings. No trail maintenance was ever observed. Rails were regularly seen using the runways, which probably facilitate walking through the dense *Pteridium*. Ten captures in 10 days (2 adults and 6 juveniles) were made with a box-trap set in the same location on one runway.

On 2 occasions juveniles were seen climbing 0.5 m above the ground, one in a *Miconia* bush and the other in a mat of dead ferns. Both seemed fairly adept at moving up and along stems and branches, often stepping from one to another. One bird fed while hanging upside-down from a fern. An adult kept in a cage easily walked up the sides, grasping the wire mesh with its feet. Twice we observed Galápagos Rails swimming in small pools at Media Luna.

Flight.—We have 13 observations of individuals flying short distances; 6 of these were of birds flushed by the observer in open meadow. These individuals flew an average of 8 m (1–30 m). One hovered for a few sec 2.5 m above the ground in front of a mist net before flying off. When another individual was chased toward a low mist net under the *Miconia*, the bird flew 0.5 m over and 1 m beyond the net. Several times birds feeding under *Miconia* were seen to fly 1–3 m across pools and resume feeding on the opposite bank. Galápagos Rails fly with the legs hanging down. Flight appears very labored and the landing is rather awkward (Griscom [1915] described similarly weak flight for Black Rails). Once a captured adult was released by tossing it about 6 m up in the air; instead of flying off, the bird fluttered to the ground and landed heavily (uninjured) in a patch of ferns.

When Gifford (1913) compared morphological measurements of 79 Galápagos Rails and 9 Black Rails, he found that the Galápagos species had proportionately shorter wings and tail. Olson (1973) has argued that reduced powers of flight could be expected to develop in rails that colonize islands. About ¼ of extant or recently extinct rallids are flightless, and all of these are from oceanic islands (Olson 1973).

Types of vocalizations.—The Galápagos Rail has an extensive repertoire of vocalizations, including cackles, clucks, warbles, trills, and hissings, but most fall into 1 of 5 categories.

(1) Cheeping.—Chicks and juveniles in family groups cheep constantly; the rate varies from about 3 per sec to 1 every 4 sec. Once, 2 independent juveniles were seen feeding and cheeping together. Cheeping young are heard easily but are difficult to locate precisely.

(2) *Chichichichirrooo* call. This call sometimes includes an introductory phrase (1–5 sec) of several harsh, squeaky *chuh-chuh-chuh* syllables (Fig. 5a). The *chichichichirrooo* segment of the call (Fig. 5b) lasts approximately 1 sec and is usually repeated several times. The *chichichichi* syllables are rapid but distinct and at the same pitch. The *rrooo* is a quick falling slur. There is a striking similarity between this call and the *kic-kic-kerr* call of the Black Rail (see sonagrams in Kellogg 1962 and Reynard 1974). Both begin with a group of equal, distinct notes (2 or 3, in the Black Rail; 5 or 6, in the Galápagos Rail), and both end with a descending slur.

The *chichichichirrooo* call seems to be the territorial advertisement call of the Galápagos Rail. It is one of the most frequently heard calls, and it carries well for distances of several hundred meters. It is the only *L.*

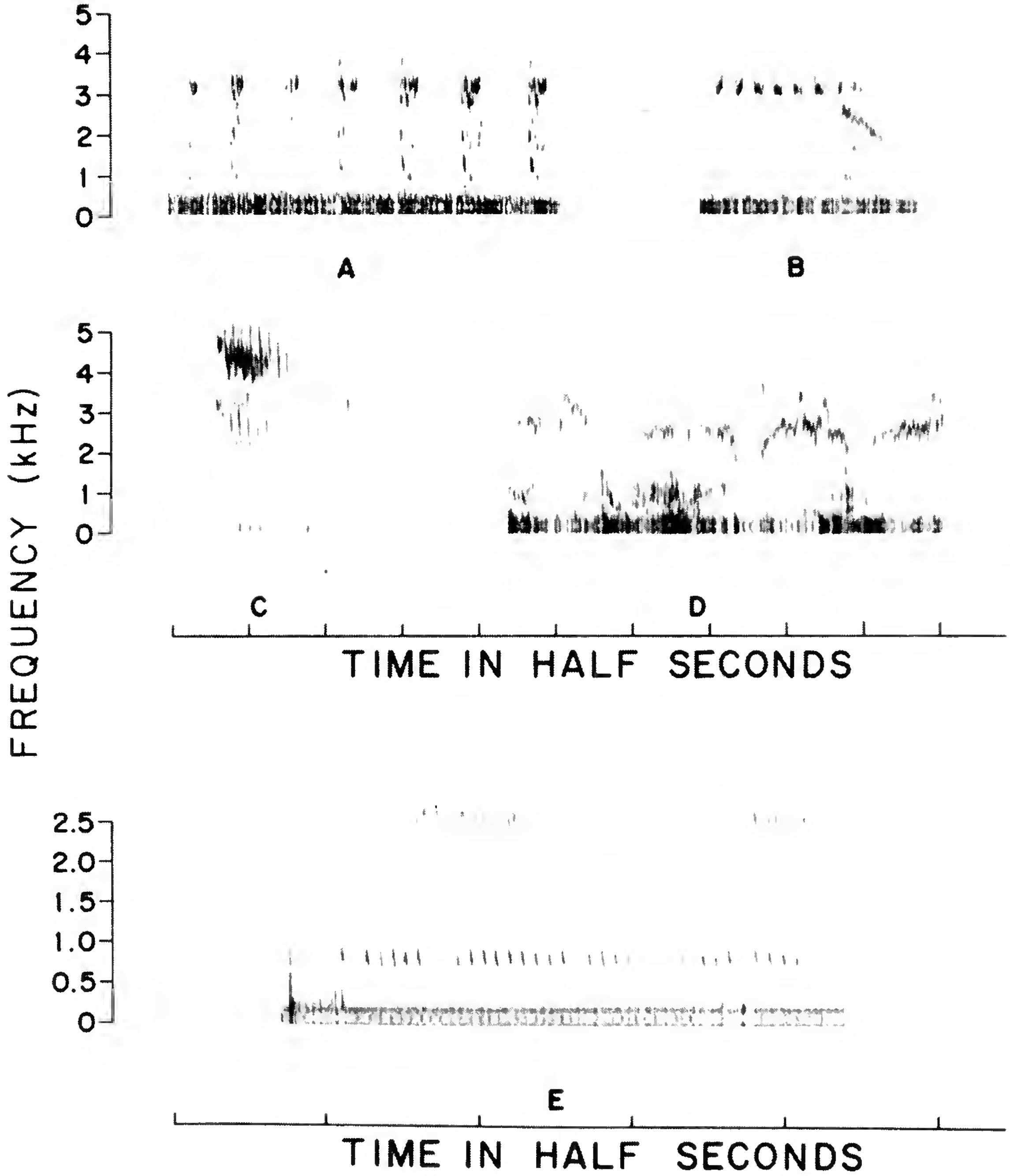

FIG. 5. Galápagos Rail vocalizations. *Chichichichirrooo* call: A. introductory syllables, B. main phrase; C. *chirr* call; D. "chatter" call; E. "rattle" call.

spilonotus vocalization we heard that does not seem to vary in its pattern. The only birds seen giving this call were adults.

(3) *Chirr* call (Fig. 5c). This call is a short (1 sec) descending trill, sometimes followed by 1 or 2 attached *chah* or *tah* syllables. We heard this call most frequently during the hot season, and recorded it only a few times in the cool season. Once a long sequence of *chirr* calling was followed by an agonistic encounter between adults.

(4) "Chatter" call (Fig. 5d). A low, breathy, wheezy chatter, this call sometimes begins slowly and usually lasts 3–9 sec.

(5) "Rattle" call (Fig. 5e). This call is a rapid, coarse rattle several sec long. One adult seen giving this call had its head pointed up at a 45° angle, with the bill opened slightly; its head and neck vibrated very rapidly as the bird called.

The "rattle" call is often preceded by the "chatter" call, but the latter is frequently heard alone. Only adults were observed giving these 2 calls; these were the vocalizations most frequently heard in response to various taped rail calls. They were also heard before and after the 2 agonistic encounters observed by the senior author.

Foot-stamping display.—The Galápagos Rail uses 2 intensities of a foot-stamping display. Mild foot-stamping consists of a bird remaining in 1 place while alternately raising and lowering the feet in a walking motion. The toes do not leave the ground and the legs are slightly bent. These displays last only a few sec and may be repeated several times, with the bird remaining in the same place or moving between displays.

In vigorous foot-stamping the bird remains stationary and drums the feet, alternately lifting each foot off the ground. The rate of drumming may be fast or slow. The body is tilted forward, held low to the ground, and remains motionless. Bouts of this display are usually longer and repeated more times than bouts of mild foot-stamping. One adult (11 June) performed 12 displays, ranging in length from 10 to 60 sec. Another (8 April) performed 1 display lasting 30 sec. In 6 observations where the position of the tail was noted, it was erect.

Juveniles (3 instances) and adults (8 instances) were seen performing the mild foot-stamping, but only adults were observed performing the vigorous foot-stamping (11 instances). All foot-stamping appeared to be directed at the observer, for the birds always looked at the observer as they displayed. In 2 instances of vigorous foot-stamping a second adult was present (the possible mate; see Adult interactions). In 1 instance a chick was present, and in 2 others an adult had been flushed from its nest. All observations suggest that mild and vigorous foot-stamping are 2 intensities of an aggressive display.

Tail erection display.—*L. spilonotus* often displays an erect tail. When an individual is undisturbed, the tail projects in line with the curve of the body. When the tail is erect, it is cocked at 45 to 90° to the horizontal. Once a bird with its tail erect also fanned the tail feathers in a semi-circle.

If the observer moved suddenly, a rail would flip its tail up as it scurried off. Twice, when individuals were caught in a box-trap, the tail was erect as each attempted to escape. Quick, jerky movements always accompanied tail erection. The action appears to be an alarm response.

Foraging behavior.—Galápagos Rails seem to feed throughout the day. On the ground, the rails have a very characteristic feeding pattern. When undisturbed they walk with tail down and dart their head to either side. They obtain food only with the bill: no rail was ever seen scratching the ground with its feet. With each dart of the head these birds jab their bills rapidly into the litter, picking up leaves and twigs and tossing or pushing them aside with the bill. They also take items off stems and frequently poke their bills into clumps of moss and other epiphytes on the trunks of *Miconia.* Several times birds were seen standing on tiptoe, jabbing the bill at something on the underside of a dead *Pteridium* frond. Twice we saw rails climb 0.5 m above the ground to forage.

At Media Luna rails frequently forage around pools, streams, and small patches of *Sphagnum* bog. The birds also wade into the water, sometimes breast-deep; they dart their heads at the surface and apparently obtain food there. Once a rail waded to a depth of several cm, picked a dead dragonfly from the surface, and carried it to shore. Generally, however, the items taken from the surface of pools and streams were too small for us to identify at a distance.

Young Galápagos Rails generally obtain their food from their parents. At 2 nests Tui De Roy (pers. comm.) saw adult *L. spilonotus* feeding insects and spiders to chicks in the nest. In 9 of the 10 observations we made of chicks feeding, an adult fed the chick (once a chick picked up something by itself and ate it). Once a chick stooped down in front of the adult, pointed its bill up, and cheeped much faster than normal; it was then fed by the adult. In 1 family, both parents were seen feeding the young; Craig MacFarland (pers. comm.) has also seen 2 adults cooperatively feeding a brood. Juvenile Galápagos Rails forage for themselves: we never observed feeding of juveniles by adults.

Behavior of family groups.—*L. spilonotus* chicks leave the nest soon after hatching. The senior author found 2 dry chicks, 1–3 days old, in a nest he had been monitoring; both chicks ran away into the surrounding grass. The 1 chick captured weighed 9 g. A free-ranging brood examined elsewhere consisted of chicks the same size or smaller (2 weighed 9 g; 2 weighed 8 g).

Once out of the nest, young Galápagos Rails stay with their parents until they are nearly the size of adults. A family with chicks moves as a cohesive group, 1 or both of the parents staying with the chicks. As the group moves, the adults cluck and the chicks maintain a constant cheeping. During approximately 2 h of observation, the formation of 1 family with 5 chicks changed frequently. At times all the chicks were behind 1 adult, the other parent moving some distance away. At other times the family split into 2 groups, each adult leading 2 or 3 chicks.

When we approached broods of Galápagos Rails, the chicks exhibited a characteristic running and freezing behavior. The parents, however, often remained nearby, circling the area and foot-stamping. On 3 different occasions, a captured chick cheeped loudly, and the parents immediately approached the investigator. Once both parents came right to the investigator's foot and remained there, 1 bird spreading its wings and calling. Another time a single adult approached the investigator in a series of 4 quick bursts of running, each ending with a spreading of the wings and a pronounced hissing call (the only time this call was heard); when the bird reached a point 0.5 m from the author it turned suddenly and ran 3 to 4 m away and repeatedly circled the area. On several other occasions, however, the adults did not approach when captured chicks cheeped loudly.

Compared to families with chicks, families with juveniles move in much looser groups. Large juveniles, like chicks, cheep constantly. A family unit can remain intact even when the juveniles are nearly adult size. Three families with 35–36 g juveniles were seen. Probable dissolution of 1 family group was recorded in 1974. On 5 March a group of 2 adults and 3 large juveniles (1 banded) was seen. Four days later the banded juvenile, which then weighed 36 g, was followed as it foraged with another large juvenile; no adults were observed. This bird was again seen on 24 March, apparently feeding by itself.

Adult interactions.—We observed a number of adult interactions (in the absence of a brood), but we were unable to distinguish sexes or breeding status of the birds. Several observations involved apparently mated pairs. On 11 June an exchange of calls was heard; soon after, an adult rail came into a small clearing and fluttered its wings violently (the only time this behavior was seen). It then entered an adjacent patch of ferns, where it joined a second adult. The 2 subsequently crossed the clearing, one after the other. Six min later the smaller bird brought a caterpillar and gave it to the larger one. Another pair (also seen 11 June) stayed within 3 cm of one another; 1 of these birds repeatedly foot-stamped toward the observer, and both preened vigorously. Then they touched bills and resumed preening. After a short interval the rails stood slightly apart and one preened the other's neck.

We observed 3 instances of fighting between adults. On 12 February, 2 rails were heard *chirr*-calling repeatedly from opposite sides of the ravine at Media Luna. Then, 1 adult quickly crossed the ravine, with its tail up and head down, in the direction of the second bird. A fairly large rail, presumably the second bird, then walked out of cover, followed by the first (considerably smaller) bird. The smaller one overtook the larger, and a fight ensued, the details of which were not seen. A repeated squeaking was heard, and 1 bird chased the other, attacking it with its claws. The larger bird moved away, and the smaller one *chirr*-called. Eventually the small individual crossed to the opposite side of the ravine and began moving along the bank, calling. Then, what was apparently a third adult flew across the ravine to the small individual, and a short fight ensued.

Fighting was again observed 1 June, after a tape of recorded rail calls was played. Two adults circled the recorder together, giving "chatter" and "rattle" calls before disappearing. Five min after the tape ended, 1 rail appeared at the edge of a small clearing in front of the recorder and looked toward it. A second adult appeared on the opposite edge of the clearing, about 1.5 m away. It hesitated, then moved rapidly toward the first bird. It ran with head down, head and wings held close to the body, and body low to the ground, and rammed the other bird with its bill. Both rails then moved rapidly into cover nearby. They made no vocalizations during the whole sequence.

On 12 September 1975, fighting followed the playing of recorded *chichichichirrooo*, "chatter", and "rattle" calls. Two different fights occurred, each between 2 birds; loud "chatter" and "rattle" calls followed both fights.

Home range and territory.—Fig. 6 shows mapped movements of adult rails in the Media Luna study area. These records are not strictly comparable among birds. Some individuals were only followed on 1 day, while others were sighted repeatedly over a span of months. Also, the study area was not sampled equally; observation was much easier around the pools. All sightings occurred from January through June (except 1 observation on 14 December). Home ranges may change later in the cool season.

The home ranges of adults, or mated pairs of adults, appear not to overlap. We never observed more than 2 adults foraging together. For only 1 bird (R-Wh) did we obtain an idea of the complete adult home range (Fig. 6). The greatest distance between R-Wh sightings was 132 m. During the 3 months this individual was followed, it raised 2 broods. A juvenile from one of the broods later occupied an area contiguous to the parents' home range. The observed ranges of juveniles were smaller than those of adults.

The possibility of territoriality was investigated using various tape-recorded *L. spilonotus* calls in a series of 31 tests. Responses, mainly "chatter" and "rattle" calls, were elicited in 24 tests. In 10 cases, it was certain that at least 2 rails called. At times the birds called independently:

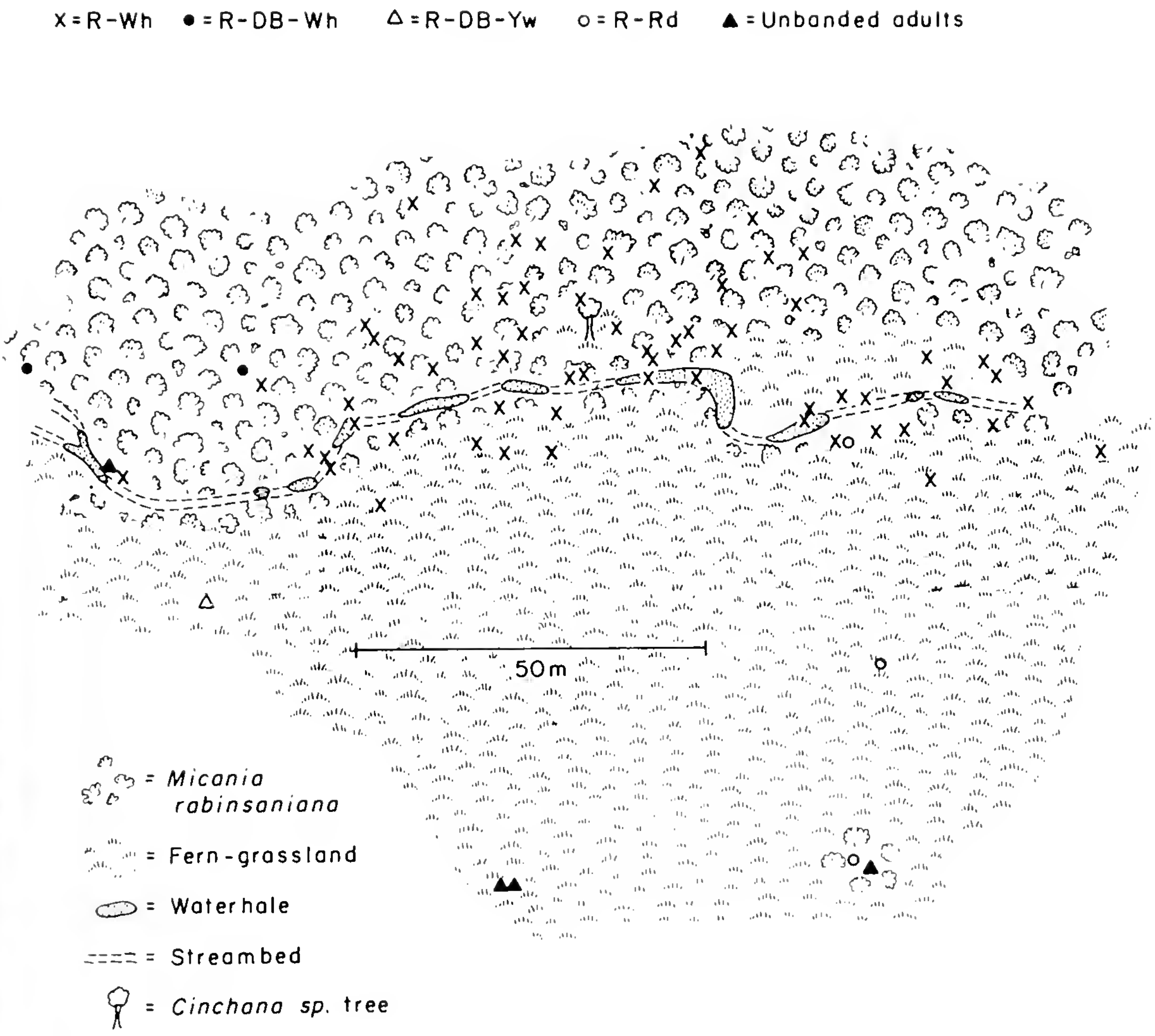

FIG. 6. Mapped sightings of adult Galápagos Rails (the stream bed runs between the west base of Media Luna and an adjacent fern-sedge meadow).

sometimes they called simultaneously, or one began calling and the other joined in. Such duet responses to taped calls have also been elicited from Clapper Rails (*Rallus longirostris*) (Tomlinson and Todd 1973) and Sora (*Porzana carolina*) and Virginia (*R. limicola*) rails (Glahn 1974).

In 11 of the tests, rails approached the recorder; all but 1 were adults. In 3 tests, 2 adults were seen together. Adults generally circled the tape recorder, looking at it or peering from side to side, calling, and occasionally foot-stamping. The 1 juvenile merely looked at the machine. Once a fight occurred between 2 adults shortly after the tape ended. No controls were used, such as playing recorded calls of other species; therefore we do not know if rails responded to the calls themselves or merely to a strange sound in their area.

The home range data and results of these tests suggest that Galápagos Rails are territorial. Possibly both members of mated pairs defend the territory, at least by calling.

CURRENT STATUS OF THE GALAPAGOS RAIL

On Santa Cruz, the population of Galápagos Rails does not seem to be in danger. These birds are fairly common around agricultural lands in the moist area; the only man-produced habitat that appears inimical to them is over-grazed short-grass pasture. The Galápagos National Park now includes most of the remaining *Miconia* belt, *Scalesia* forest, and almost all of the fern–sedge zone; therefore much of the remaining natural rail habitat is protected.

With the exception of Fernandina, all of the islands on which *L. spilonotus* occurs also have introduced mammals. Most of these mammals are potential predators or competitors of the Galápagos Rail (e.g., the goats on Pinta). Rail populations should be censused systematically; an assessment line using tape-recorded rail calls would be the most practical method.

SUMMARY

The endemic Galápagos Rail, *Laterallus spilonotus*, originally occurred in mangrove and moist highland habitats in the Galápagos Islands, Ecuador. Today it is restricted to high moist areas on 7 islands. We report the results of a 10-month field study of this species' behavior and ecology on Santa Cruz Island.

Breeding records extend from the middle of the cool season (September) to the end of the hot season (April). The covered nests have a side entrance and are built on the ground. Recorded clutch-size ranges from 3 to 6; both adults incubate the eggs and feed the chicks. One bird was observed with 2 sequential broods in 1 season. The juveniles have brown to orange irises and a patch of white on the bill; adults have crimson irises and completely black bills. One breeding year-old bird was observed. *L. spilonotus* feeds primarily on invertebrates. The only recorded predation was by a domestic dog.

Galápagos Rails are primarily diurnal and are relatively easily observed. They are basically ambulatory; we saw only occasional short and apparently labored flights. The 5 most common vocalizations are: cheeping (chicks and juveniles); *chichichichirrooo* call (the probable territorial advertisement); *chirr* call (heard most often in the breeding season); and "chatter" and "rattle" calls (the usual responses to taped calls; also associated with agonistic encounters). Two characteristic displays are foot-stamping and tail erection.

Both parents remain with the young until the late juvenile stage. Adults feed chicks, but all juveniles observed fed themselves. We never saw more than 2 adults foraging together. Adult home ranges appear not to overlap.

The Santa Cruz population seems stable; the effects of exotic predators and competitors on all Galápagos Rail populations should be examined.

RESUMEN

La endémica gallineta galapagueña ("pachay"), *Laterallus spilonotus*, se encontraba originalmente en manglares y en medios altos y húmedos en las Islas Galápagos, Ecuador. Hoy día existe solamente en las zonas altas y húmedas de 7 islas. Se exponen en el presente trabajo los resultados de los estudios efectuados durante 10 meses sobre la ecología y el comportamiento de esta especie en la Isla Santa Cruz.

Existen observaciones de reproducción desde los mediados de la estación de garúa (septiembre) hasta los fines del invierno (abril). Los nidos tapados tienen una entrada a un lado y son construidos sobre el suelo. Nidadas observadas consistieron en 3 hasta 6 huevos; los dos adultos incuban los huevos y dan de comer a los polluelos. Un individuo tuvo dos nidadas sucesivas en una estación. El iris de los jóvenes es pardo o naranjado, y hay una mancha blanca en el pico; el iris de los adultos es carmesí, y el pico es totalmente negro. Se observó un individuo de un año de edad que había reproducido. *L. spilonotus* come principalmente invertebrados. En el único caso observado de predación, un perro domesticado mató un pachay.

Los pachay son principalmente diurnos y se los puede observar relativamente facilmente. Son básicamente ambulatorios; observamos solamente de vez en cuando vuelos cortos que parecieron penosos. Las 5 vocalizaciones más frecuentes son: el pío (polluelos y jóvenes); el canto *chichichichirrooo* (probablemente el canto territorial); el canto *chirr* (que se oye más frecuentemente durante la época de reproducción); y los cantos "parloteo" y "traqueteo" (las respuestas comunes a cantos grabados; también asociados con encuentros agresivos). Dos exhibiciones de conducta características son golpes en el suelo con las patas y levantamientos de la cola.

Los dos padres quedan con los jóvenes hasta que son casi adultos. Los adultos dan de comer a los polluelos, pero todos los jóvenes observados se alimentaron a sí mismos. Nunca vimos más de dos adultos buscando comida juntos. Aparentemente las áreas donde viven los adultos no se traslapan.

La población de Santa Cruz parece estable. Quedan por examinar los efectos de predadores y competidores introducidos en todas las poblaciones de *Laterallus spilonotus*.

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EXPERIMENTS ON POPULATION REGULATION IN TWO NORTH AMERICAN PARIDS

FRED B. SAMSON AND STEPHEN J. LEWIS

Two major hypotheses to explain annual fluctuations of avian populations have emerged from long-term studies of the Great Tit (*Parus major*) in England (Perrins 1965, Lack 1966) and the Netherlands (Kluijver 1951, 1971; Kluijver and Tinbergen 1953). Lack (1966) argued that annual changes in Great Tit breeding populations reflected mortality of immatures due to starvation between leaving the nest and early winter, whereas Great Tit numbers in Holland according to Kluijver (1951, 1971) were regulated by a behaviorally induced emigration in fall rather than by direct starvation. Although natality often is variable in Great Tit populations from year to year, neither hypothesis considers variation in reproduction directly responsible for changes in breeding numbers. Nor does it appear that spring territory acts as a major density dependent factor regulating a population of the Great Tit (Krebs 1971) or of 2 other European parids, the Crested Tit (*P. cristatus*) and Willow Tit (*P. montanus*) (Cederholm and Ekman 1976), but controversy remains (Slagsvold 1975).

Although several North American parids have been intensively studied (Odum 1941, 1942; Dixon 1963; Smith 1972, 1976; Glase 1973), it remains unclear what factors influence annual changes in their numbers. The purpose of this study was to experimentally test Lack's and Kluijver's hypotheses on populations of the Black-capped Chickadee (*P. atricapillus*) and Tufted Titmouse (*P. bicolor*) in central Pennsylvania.

STUDY AREA AND METHODS

The study area of ca. 60 ha was centrally located in the 2800-ha Stone Valley Experimental Forest, Pennsylvania State University, 17 km southeast of State College, Huntington Co., Pennsylvania. The mature forest on the study area of black oak (*Quercus velutina*), white oak (*Q. alba*), red maple (*Acer rubrum*), white pine (*Pinus strobus*) and gray dogwood (*Cornus racemosa*) is interspersed with steep slopes, gullies and intermittent streams.

The 3 phases of the study were: (1) to describe under natural circumstances the location and size of breeding territories and winter flocks; (2) to test Lack's hypothesis by providing supplemental food from late summer through winter and observing responses of fall–winter flocks and subsequent breeding populations; and (3) to examine Kluijver's hypothesis by conducting a fall removal experiment and noting the timing and extent of recolonization.

During phase 1 from September 1974 through May 1975, 18 titmice and 26 chickadees were trapped and fitted with a USFWS numbered aluminum band. Thirteen titmice and

14 chickadees were marked with unique combinations of colored plastic leg bands. We used mist nets and 1-cell Potter traps baited with sunflower seeds to capture birds. Birds were sexed following Wood (1969) supported by our own measurements of 42 Black-capped Chickadee and 39 Tufted Titmouse museum specimens. Aging was by skull examination (Miller 1946). In addition to the banding records, we mapped all observations of color-marked birds to describe the spatial organization and membership of 3 winter chickadee flocks (designated BFL 1, BFL 2, and BFL 3) and 3 winter titmouse flocks (designated TFL 1, TFL 2, and TFL 3). Other flocks were located but 6 was the maximum that could be studied intensively. The number of breeding territories was estimated each spring by mapping singing males (Kendeigh 1944). From March to May we conducted 6 censuses in 1975, 7 in 1976 and 4 in 1977. Even though color-marked in fall and winter, females were difficult to observe in spring and were not always individually identified.

For phase 2, we fed mealworms (*Tenebrio* sp.) and sunflower seeds beginning in mid-July 1975. Mealworms were not consumed by the parids, but sunflower seeds were, starting in early September 1975. From this date to 1 March 1976, a feeder holding 11.3 kg of sunflower seeds, suspended by several fine wires or attached to a 3-m pole equipped with a squirrel guard, was placed within the range of flocks BFL 1, BFL 2, TFL 1, and TFL 2 as defined in the 1974–75 winter. Because of the overlap of BFL 1 and TFL 1, and BFL 2 and TFL 2, each flock had access to 2 feeders. Feeders were checked at least weekly and more frequently in cold weather. They were moved each week to a new location. Over 700 kg of sunflower seeds were fed to the parids and other species. Between September 1975 and April 1976, we placed USFWS bands on an additional 31 chickadees (27 color-marked) and 17 titmice (17 color-marked).

In phase 3 from September 1976 to January 1977 we bi-weekly removed all flock members that could be captured within a morning. Seven 1-cell Potter traps, usually baited on the preceding day but left locked open, were placed in an overlap of BFL 1 and TFL 1 and 6 within the ranges of BFL 2 and TFL 2. Trapped birds were marked and displaced 17 km. No titmouse or chickadee returned.

Availability of arthropod food for the Black-capped Chickadee and Tufted Titmouse during the breeding season was measured in a mature forest similar to Stone Valley 17 km northeast of the study area. Four sweep net (0.3 m diam.) samples of 50 sweeps each were taken in the shrub–lower canopy every 10 days from May into September 1976. These arthropods were frozen, dried at 50°C and weighed.

RESULTS

The 3 chickadee flocks marked in the fall and early winter of 1974 included 8 birds in BFL 1, 7 in BFL 2, and 8 in BFL 3. Membership in these flocks remained fairly constant from October through January with only 1 male in BFL 1 and 1 in BFL 2 disappearing in mid-winter. The ranges of the 3 flocks did not overlap (Fig. 1) except for 1 male of BFL 1 which was captured in all 3 flock ranges. Chickadees foraged in groups of 6 to 8 until late February when males began to establish territories. Four males from BFL 1 and 3 males from BFL 2 used nearly half of their respective winter flock ranges to establish breeding territories (Fig. 1). One of 4 males of BFL 3 defended a territory that extended beyond the BFL 3

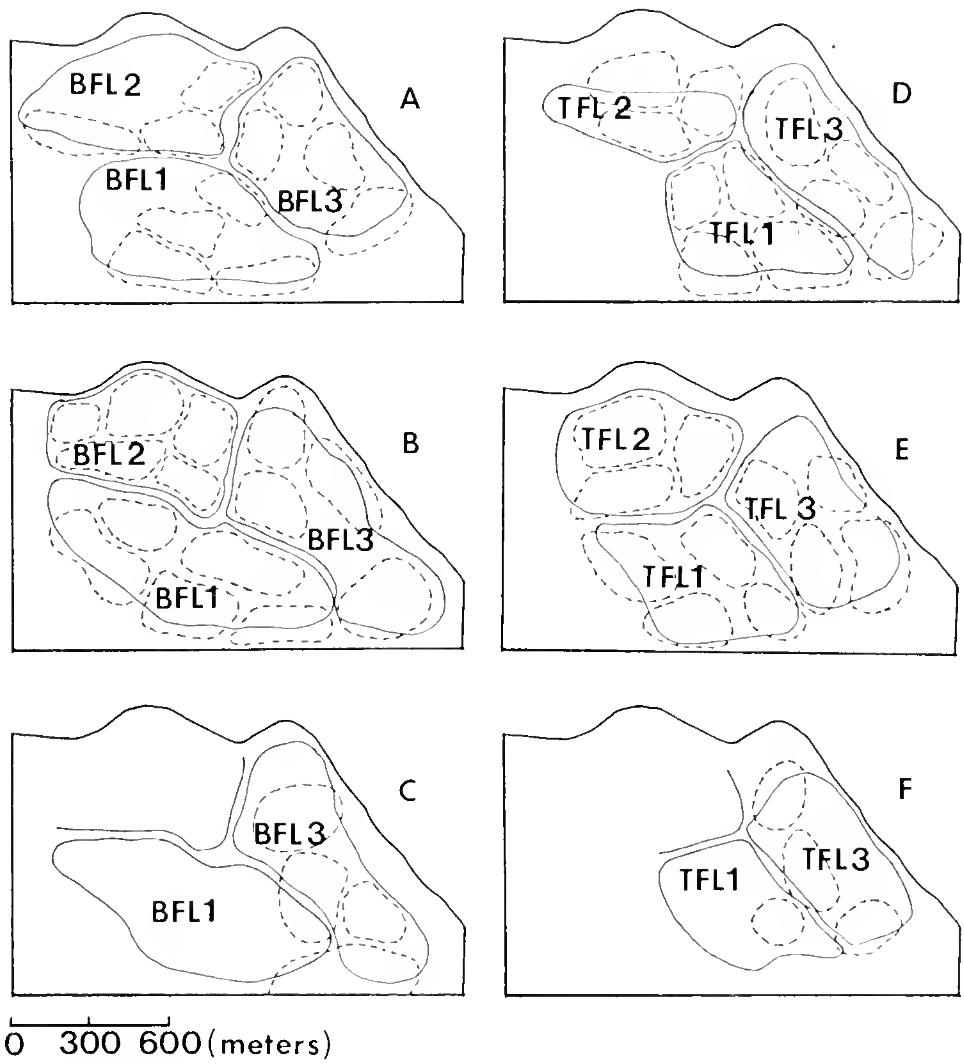

FIG. 1. Spatial arrangement of winter flocks and breeding territories of Black-capped Chickadee in: (A) winter–spring of 1974–75; (B) winter–spring of 1975–76; (C) winter–spring of 1976–77; and of Tufted Titmouse in: (D) winter–spring of 1974–75; (E) winter–spring of 1975–76; and (F) winter–spring of 1976–77. A winter flock range is outlined by a solid line and a breeding territory by a dashed line. Flock abbreviations (BFL 1, TFL 1, etc.) are defined in the text. Flocks BFL 1, BFL 2, TFL 1, and TFL 2 were experimental populations in 1975–76 and 1976–77 and BFL 3 and TFL 3 served as control populations.

winter flock range even though vacant habitat within the winter range was available.

Fig. 1 shows the spatial relationships of the 3 titmouse flocks in the winter of 1974–75. From October to mid-February, 7 birds were in TFL 1, 5 in TFL 2, and 8 in TFL 3. These flocks were mutually exclusive throughout the winter. Titmice most often foraged in groups of 2 or 3 but no group covered the entire flock range. In late February and early March, titmouse flocks broke up when males began to exhibit territorial behavior. Four males from TFL 1 established territories that almost entirely overlapped with their winter flock range (Fig. 1). Similarly 3 males of TFL 2 created territories that included a major portion of their winter flock range. An unmarked male of unknown origin and 3 marked males of TFL 3 defended territories that included most of the TFL 3 winter range.

Fall–winter feeding experiments.—When testing Lack's hypothesis, Krebs (1971:14) pointed out that "if winter (supplemental) feeding had a measurable effect, the breeding density in the experimental area should have a larger increase relative to the control area." Supplemental feed (sunflower seeds) was provided to BFL 1 and BFL 2 and TFL 1 and TFL 2 from early September 1975 through late February 1976. This feeding ceased 1 March 1976 to prevent the acceleration of breeding caused by supplemental food as noted in the Great Tit (Källander 1974). BFL 3 and TFL 3 served as control flocks.

Both experimental chickadee flocks (BFL 1 and BFL 2) were larger as observed on 25 weekly censuses between 8 September 1975 and 6 March 1976, relative to the control flock BFL 3. BFL 1's flock size of 15 (8 in 1974–75) and BFL 2's of 13 (7 in 1974–75) were larger than the 8 for the control BFL 3 (8 in 1974–75). Four chickadees in BFL 1, 4 in BFL 2, and 4 in BFL 3 were banded in the preceding winter. Two first-year birds from BFL 2, 1 first-year bird from BFL 2, and 1 adult from BFL 3 disappeared during this winter.

In the spring of 1976, 4 males from BFL 3 established territories in a spatial arrangement similar to the preceding spring (Fig. 1). Five males of BFL 2 defended territories which included portions of the BFL 2 winter range vs 3 males in the 1975 spring. The breeding density in or near the winter range of BFL 1 increased from 4 males in the spring of 1975 to 5 in 1975.

Neither TFL 1 nor TFL 2 increased in number relative to the control TFL 3 during the supplemental feeding. TFL 1 as observed on 25 weekly censuses beginning 8 September consisted of 8 birds, TFL 2 had 8 and TFL 3 had 6 birds in the 1975–76 winter compared with 7, 5, and 8, respectively, for the 1974–75 winter. Five birds from TFL 1, 3 from TFL 2, and 3 from TFL 3 had been banded in the preceding winter. One female from TFL 2 and 1 male from TFL 3 disappeared during the winter. No major change was evident in the breeding density from 1975 to 1976 (Fig. 1). Similar to the preceding year, 4 males from TFL 1, 3 from TFL 2, and 4 from TFL 3 established territories that encompassed at least part of their respective winter flock range.

Fall removal experiments.—During the breeding season and after the spring migration, the experimental removal of established territorial males

TABLE 1

SUMMARY OF EXPERIMENTAL REMOVAL OF TUFTED TITMICE

	Flock 1		Flock 2	
Month	No. trap hours[1]	No. removed	No. trap hours[2]	No. removed
Sept.	53.5	3 (1)[3]	45.5	4 (1)
Oct.	95.0		80.9	3 (2)
Nov.	229.2	2	195.3	4 (3)
Dec.	90.2		76.8	
Jan.	100.0		85.3	
TOTAL	567.9	5 (1)	483.8	11 (6)

[1] Seven 1-cell Potter traps, includes time when removing birds from traps.
[2] Six 1-cell Potter traps, includes time when removing birds from traps.
[3] Number of immatures in parentheses.

followed by their rapid replacement has been interpreted to show that territorial behavior limits a local population density (Watson and Moss 1970, Krebs 1971, Thompson 1977). If, as suggested by Kluijver (1951, 1971), tit populations are regulated by fall territorial behavior, birds removed from fall flocks should be replaced by individuals displaced by that or other intraspecific strife associated with dominance hierarchies. From September 1976 through January 1977, trapping efforts attempted to remove all chickadees and titmice from BFL 1, BFL 2, TFL 1, and TFL 2, respectively, while BFL 3 and TFL 3 served as controls.

Six Black-capped Chickadees from BFL 1 and 7 from BFL 2 were removed in September 1976. No additional chickadees were captured from October 1976 through January 1977 during 567.9 trap hours in the range of BFL 1 and 483.8 trap hours in the range of BFL 2. Three of 6 in BFL 1 and 3 of 7 in BFL 2 were juveniles. Two of 3 adults in BFL 1 and 3 of 3 in BFL 2 had been banded in a preceding winter. In the subsequent breeding season the number of males (4) establishing territories in BFL 3 remained constant from the preceding 2 springs, but no territories were established in the winter range of BFL 1 (vs 4 in 1975 and 5 in 1976). The range of BFL 2 was not censused.

Four of 5 tits removed from TFL 1 were more than 1 year old as were 5 of the 11 birds removed from TFL 2 (Table 1). Three of 4 adults in TFL 1 and 4 of 5 in TFL 2 were banded in a preceding winter. Only 1 titmouse established a territory in the range of TFL 1 (Fig. 1), vs. 4 in 1975 and 1976, but the range of TFL 2 was not censused. It is possible the male defending a territory in the range of TFL 1 was a member of TFL 3,

TABLE 2

MEAN DRY WEIGHT AND MEAN NUMBER OF ARTHROPODS PER MONTH COLLECTED IN SWEEP NET SAMPLES AT APPROXIMATELY 10-DAY INTERVALS FROM 5 MAY TO 20 SEPTEMBER 1976

Month		Dry weight (g)		Number	
		x̄	SD	x̄	SD
May	(12)[1]	0.094	0.065	33.8	11.8
June	(12)	0.087	0.046	36.0	10.0
July	(12)	0.145	0.108	33.8	3.8
Aug.	(8)	0.059	0.029	36.9	8.6
Sept.	(8)	0.076	0.036	64.8	12.5

[1] Number of 50-sweep samples per month in parentheses.

but tits rarely descended below 15 m during the breeding season, making individual recognition difficult. Three males in 1977, as compared to 4 in 1976, defended breeding territories in TFL 3.

Food resources.—Table 2 summarizes the dry weight and number of arthropods collected at approximately 10-day intervals from 5 May to 20 September 1976. There was no significant difference in mean weight among the 5 sample periods (2-way ANOVA, F = 1.44). The heaviest samples were collected in late July and early August with a substantial decline in biomass during late August and early September. Numbers of arthropods per 50 sweep samples varied greatly because of change in numbers of small Diptera and arachnids collected in some samples.

DISCUSSION

Two major questions in avian population ecology revolve around the timing and extent of mortality in relation to annual fluctuation in breeding numbers and the existence or non-existence of surplus individuals that are prevented from breeding by fall or spring territorial behavior. Lack (1966:75) contended that "annual fluctuations in the breeding populations of the Great Tit in Marley Wood were due primarily to corresponding variations in juvenile mortality before winter" with most occurring within 2 or 3 weeks of leaving the nest. Perrins (1965) provided indirect evidence supporting Lack by showing that lighter juvenile Great Tits in England apparently had lower survival rates than heavier juveniles. However, Kluijver (1966), in an experimental test of Great Tit density and early post-fledging mortality, did not support the conclusions of Lack and Perrins.

He removed 60% of the eggs of a Great Tit population breeding on the isolated Dutch North Sea island of Vieland, yet this did not affect the subsequent breeding density (Kluijver 1966, Klomp 1972).

We were not able to examine mortality during the 2 or 3 week post-fledging interval. Broods of chickadees and titmice fledged on the study area from mid-June to mid-July. Neither species exhibited the drastic decrease in height of feeding (to the level of the feeders) observed in Great Tits by Royama (1970) when young were fledged. Several factors, however, suggest juvenile mortality was minimal on the study area during this interval. In the summers of 1975 and 1976, family groups varied little in size in both species and were observed through July and August, although adults were particularly aggressive toward young in late August and September. In both chickadee and titmouse flocks in the fall of 1976, our banding indicated juveniles outnumbered adults. In the 1976 summer, arthropod biomass remained high until late August and a similar pattern presumably existed in 1975. Good juvenile survival into August has been reported in Black-capped Chickadee populations by Odum (1942), Smith (1967) and Glase (1973) but little information exists for this interval in the Tufted Titmouse (Dixon 1955, Brackbill 1970).

The role of mortality and dispersal in determining population size in late summer or fall has been considered by several authors (Snow 1958, Jenkins et al. 1963, Tompa 1964, Southern 1970). Lack (1966:79) reported a strong correlation between tit numbers and size of a fall "beechmast crop" even though the mast was available well after the post-fledging period. He further pointed out that this relationship existed in areas without beech but with other trees producing seeds in the same years as beech. Artificial winter feeding of Black-capped Chickadee flocks can be associated with increased winter numbers (Wallace 1941, Hamerstrom 1942, Odum 1942, this study). There are additional suggestions, particularly in finches and sparrows, that winter food supply is important in determining numbers of breeding birds (Newton 1964, Fretwell 1969, Pulliam and Enders 1971). However, to date the only experimental test of the effect of fall–winter food on subsequent breeding numbers is by Krebs (1971).

In Krebs' (1971) study, the numbers of Blue Tit (*P. caeruleus*) (but not Great Tit) breeding pairs per ha increased following the supplemental feeding of sunflower seeds from 1 October 1968 to 22 April 1969. He suggested 3 possible reasons Blue Tit breeding density increased after feeding: (1) food directly influenced territory size, (2) feeding increased winter survival, (3) immigration occurred from surrounding areas. We ceased feeding when vernal territorial behavior was first observed, to prevent food serving as a proximate factor influencing territorial establishment or to accelerate the onset of breeding. Feeders also were moved each week to reduce any effect of the location of feeding stations on territorial arrangements. Flock size of both species remained nearly constant from mid- or late October to February in the control year (1974–75) as well as in the control and experimental flocks in 1975–76. Smith (1967) also reported good overwinter survival in Black-capped Chickadees, and Glase (1973:241) noted that "with the exception of the disappearance of certain individuals in late August and early September, the composition of flocks found in mid-August remained constant throughout the rest of the flocking period." In the Plain Titmouse (*P. inornatus*), Dixon (1949) reported 11 of 14 (78.5%) pairs re-mated for at least 1 season which suggests a good winter survival. Condee (1970), in a winter study of the Tufted Titmouse, reported considerable movement and consistent clan (perhaps family groups) membership through a winter, but did not directly discuss survival. Rather than food serving as a proximate factor in improving winter survival, it appears to influence the degree of immigration.

Whether juvenile chickadees banded in September or October 1975 were raised by pairs breeding on the study area is not known. The fall ratio of juveniles to adults in experimental flocks increased from 1:1 in BFL 1 in 1975 to 2.75:1 in 1976, and from 0.75:1 on BFL 2 in 1975 to 2.3:1 in 1976, suggesting either a reduced dispersal or increased immigration. Although supplemental feeding on BFL 1 and BFL 2 increased winter numbers of chickadees 87.5% (8 to 15) and 85.7% (7 to 13), respectively, breeding density increased only 25% (4 to 5) and 66% (3 to 5). It is not clear why the increase in breeding density did not parallel the increased winter flock size; those marked males failing to obtain a territory were not observed again. Smith (1967:357) described a "sharply defined period of high mortality, emigration, or both" when flocks break up and territorial behavior begins in spring and a similar pattern appeared to exist in our experimental chickadee populations.

Watson and Jenkins (1968), in a series of carefully designed autumn removal experiments, reported that breeding numbers of Red Grouse (= Willow Ptarmigan) (*Lagopus lagopus*) are influenced by territorial behavior in the preceding fall. When a territorial male was removed in fall, he was rapidly replaced. However, if removed in spring, males were replaced rarely or not at all, since surplus cocks die during late autumn and winter. Other experimental evidence based on removal experiments to explain the effect of fall territory on breeding numbers is lacking, even though the removal procedure has been used to define the effect of spring territory on breeding numbers (Orians 1961, Bendell and Elliott 1967, Krebs 1971, Zwickel 1972, Bendell et al. 1972, Samson 1976, Thompson 1977).

In this study, we planned to remove all individuals of both species every 2 weeks to determine if replacement would occur in either species and to ascertain the size and sex, and age structure of any replacement population. All chickadees were removed on 13 and 19 September from BFL 1 and BFL 2, and they were not replaced. Other species, including 6 White-breasted Nuthatches (*Sitta carolinensis*), were caught in November within BFL 1's range. In BFL 2's range, 3 White-breasted Nuthatches, 5 Downy Woodpeckers (*Picoides pubescens*) and 1 Blue Jay (*Cyanocitta cristata*) were caught in November. This trapping and our previous success in capturing chickadees and titmice suggest our trapping techniques were unable to detect subsequent replacements.

Condee (1970) reported that Tufted Titmice in winter in central Pennsylvania formed clans of 3 to 6 individuals. Each clan had a winter territory and, although some overlap was evident, there were no conflicts reported. Also in Pennsylvania, Gillespie (1930) reported winter groups of 2 to 6 titmice with nearly exclusive ranges and Nice (1933) reported winter flocks with definite ranges. Van Tyne (1948) and Dixon (1955) reported that titmouse flocks may consist of 1 or more pairs although a pair may only occasionally be a member of a flock. Our observations agree with Van Tyne and Dixon even though no pair traversed our entire flock winter range.

In removing titmice, 7 (TFL 1) or 6 (TFL 2) traps were all located within a 15 m radius and not necessarily within the range of a group of tits. This may have influenced the pattern of removal involving a 6-week period in TFL 1. The origin of the 1 adult and 3 young removed in November from the range of TFL 2 is not known and they may have been replacements. It is also possible that the unmarked adult replaced a breeder from TFL 2 and raised the young within the range of TFL 2.

The level of replacement noted in removal experiments conducted in spring on other species, however, was not evident in either chickadee or titmouse flock ranges. Examples include the rapid replacement of 27 of 28 (96.4%) Great Tits removed by Krebs (1971), 211 (approximately) of 204 (103.4%) Blue Grouse (*Dendragapus obscurus*) by Zwickel et al. (1972), and 27 of 40 (67.5%) male Yellow-breasted Chats (*Icteria virens*) by Thompson (1977). In the cases of the Great Tit and chat, the authors provide convincing evidence of nearby territory holders expanding holdings, re-occupying abandoned territories, or moving from marginal to more favorable habitat, with little or no evidence for the existence of a surplus or nonbreeding population. Our fall removal experiments also indicate the nonexistence of surplus flocks and, more importantly, that winter flock size and the subsequent breeding density appeared to be established by the preceding fall. They do not fully clarify the role of intraspecific strife in autumn, for it may have had a major impact on the emigration and mortality before the onset of our experimental removals.

Summarizing, if one removes birds in mid-September there are no chickadee and few titmouse replacements. Thus, there appears to be an interval of dispersal prior to or during late August and early September followed by considerable mortality or decreased movement (i.e., no recolonization). This dispersal in 1976 preceded the decrease in food as measured by arthropod biomass. In nearly all cases those surviving this interval were able to attempt to breed the subsequent spring. Thus, Lack's (1966) hypothesis that a period of mortality accompanying the decline in summer food sources influences subsequent breeding densities may explain the lack of replacements in this study, but we have no proof of individual mortality. Whether, as suggested by Kluijver (1951, 1971), intraspecific strife in autumn has a major impact on emigration and mortality needs further investigation, principally through removal experiments beginning before early to mid-August when food decreases and aggressive behavior increases.

SUMMARY

Black-capped Chickadees in fall formed flocks that were nearly exclusive in membership. At end of winter, flocks broke up when males established territories. Similarly, Tufted Titmice in fall formed flocks that remained together through winter, yet no pair traversed the entire flock range. Black-capped Chickadees, but not Tufted Titmice, responded to supplemental feeding with a substantial increase in fall–winter flock size but only a minor increase in breeding density. Replacement following fall removal experiments did not occur in the Black-capped Chickadee and was limited in the Tufted Titmouse. We interpret these results as possible support of Lack's hypothesis for regulation of an avian population, but they did not resolve the role of late summer–autumn intraspecific strife in regulation of a parid population as suggested by Kluijver.

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HABITAT USE BY THE BLACKPOLL WARBLER

Douglass H. Morse

Habitat use and partitioning by wood warblers in northern coniferous forests have attracted considerable interest (MacArthur 1958; Morse 1968, 1971, 1978). Studies have documented and compared the foraging patterns of several species: Magnolia (*Dendroica magnolia*), Cape May (*D. tigrina*), Yellow-rumped (*D. coronata*), Black-throated Green (*D. virens*), Blackburnian (*D. fusca*), Bay-breasted (*D. castanea*), and Parula (*Parula americana*) warblers. However, little precise information exists upon the exploitation patterns of Blackpoll Warblers (*D. striata*), although they also nest in the northern coniferous forests of eastern North America. At the southeastern limits of their breeding range, Blackpoll Warblers occur on mountaintops, and they also appear on wooded coastal islands of Maine and the Maritime Provinces (Bond 1951, Griscom and Sprunt 1957). Farther north they occur throughout the boreal coniferous forest and breed nearer to the tundra than any other warbler (Todd 1963).

This species is of particular interest, since it is morphologically extremely similar to some of the congeners mentioned above, particularly the Bay-breasted Warbler. Further, it does not appear to nest in many areas frequented by Bay-breasted Warblers, suggesting that these 2 species may exclude each other in most places. I studied the foraging patterns of Blackpoll Warblers on their breeding grounds in the White Mountains of New Hampshire, using techniques similar to those described elsewhere (Morse 1968, 1971) for other warblers. I have supplemented this information with data obtained during spring migration in deciduous forests in Maryland and in spruce forests along the Maine Coast.

STUDY AREAS AND METHODS

Study areas.—Fieldwork on the breeding grounds was carried out on Mt. Osceola, Livermore Twp., Grafton Co., New Hampshire, in June 1971 and June 1977. I gathered foraging observations in forests from about 1050 m to the summit at 1319 m. Balsam fir (*Abies balsamea*) was the predominant tree, with small numbers of white birch (*Betula papyrifera*) and red spruce (*Picea rubens*) (Table 1). The forest ranged from about 3 to 12 m in height, with heavy stunting occurring only at the very top of the mountain (Fig. 1). The only other common warbler in this area was the Yellow-rumped Warbler.

The range of Blackpoll Warblers also extended down Mt. Osceola to about 750 m. Most of this area (down to 825 m) was covered by a dense, second-growth, mixed coniferous-deciduous forest (Fig. 1, Table 1). The lowest area in which apparently breeding Blackpoll Warblers occurred consisted primarily of tall mixed forest (Fig. 1,

TABLE 1

RELATIVE ABUNDANCE (%) OF CANOPY-HEIGHT TREES IN NEW HAMPSHIRE CENSUS PLOTS[1]

	Census plot			
Species of tree	Top (1150 m)	Next to top (950 m)	Next to bottom (850 m)	Bottom (750 m)
Balsam fir (*Abies balsamea*)	97	60	4	12
White birch (*Betula papyrifera*)	3	28	70	14
Red spruce (*Picea rubens*)	–	7	16	25
Pin cherry (*Prunus pensylvanica*)	–	5	9	15
Quaking aspen (*Populus tremuloides*)	–	–	1	–
Yellow birch (*Betula lutea*)	–	–	–	23
Sugar maple (*Acer saccharum*)	–	–	–	6
Mountain maple (*A. spicatum*)	–	–	–	4
Striped maple (*A. pensylvanicum*)	–	–	–	1

[1] The 10 nearest canopy or sub-canopy trees at 10 randomly chosen sites on each census plot.

Table 1). Neither of these areas are typical of the Blackpoll Warbler's commonly reported nesting habitat (Taber 1952, Gross *in* Bent 1953, Todd 1963). Although I did not make systematic foraging observations in these areas, I censused the bird populations there.

I studied the foraging of Blackpoll Warblers in migration in Maryland during May 1977. They occur in large numbers there in mature deciduous forests while in passage, being one of the most abundant of migrants at this time. The profile of the forest in which they were observed (University Park, Prince George's Co.) is shown in Fig. 1. The commonest tree species were red maple (*Acer rubrum*), sweet gum (*Liquidambar styracifolia*), and river birch (*Betula nigra*).

Blackpoll Warblers are uncommon spring migrants in the spruce forests along the Maine Coast. I made a limited number of observations upon them there in white spruce (*Picea glauca*) forests from 1966 to 1972. The foliage profiles of these forests (illustrated in Morse 1971, 1973) are rather similar to those of the fir forest censused on Mt. Osceola (Fig. 1), although the forest is somewhat taller.

Methods.—In gathering foraging data I followed techniques described in earlier studies (Morse 1968, 1971, 1978). Briefly, I measured the time that different individuals foraged at different heights and in different parts of the tree (tips of foliage,

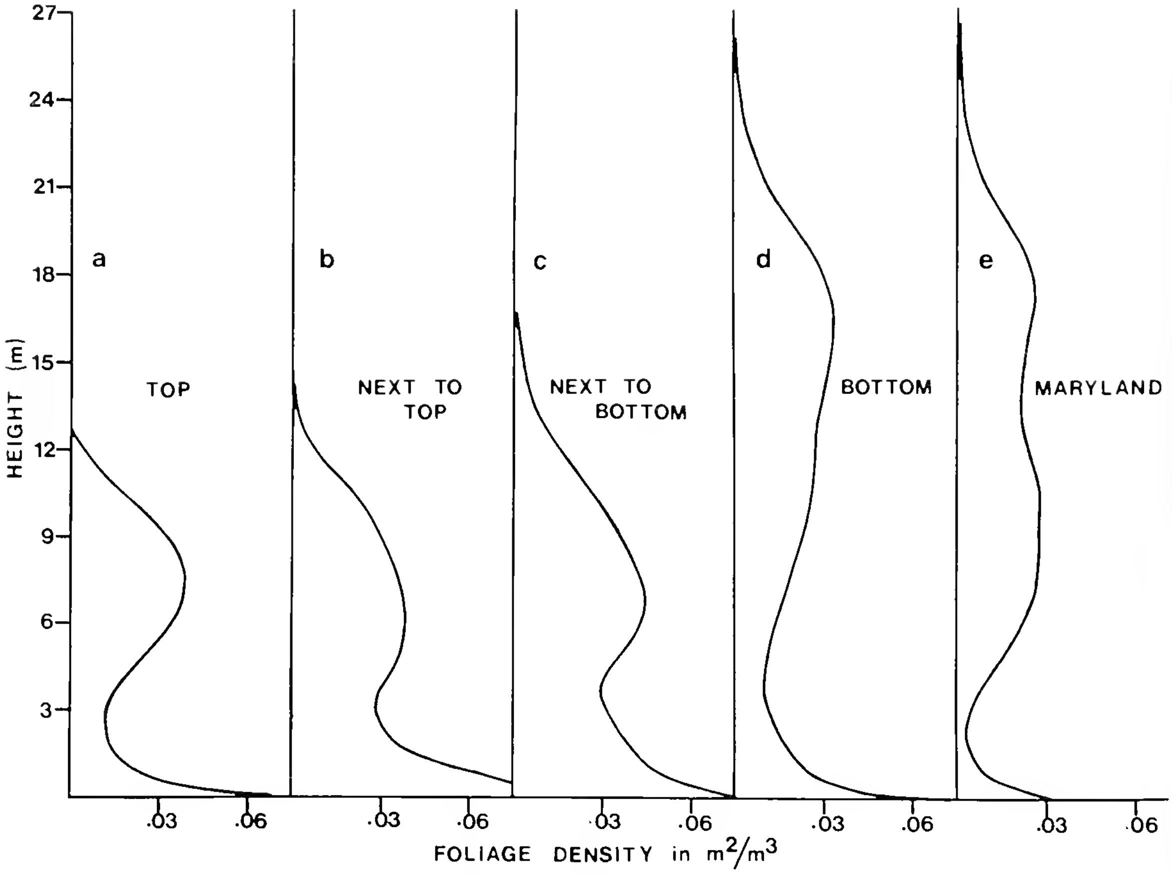

FIG. 1. Profiles of foliage in 4 census areas on Mt. Osceola (a–d); profile of foliage in Maryland study site (e). All profiles measured using techniques of MacArthur and MacArthur (1961).

inner part of limbs, etc.). I recorded a maximum of 5 min of foraging per individual, although it usually was not possible to obtain that much information before a bird was lost. I made an effort not to gather foraging data from the same general location more than once, and the results obtained come from a minimum of 25 individuals in both New Hampshire and Maryland and 8 individuals in Maine. Most of the observations were made upon males. Since I located several individuals by their songs, I checked for possible bias in the locations recorded. Data from the first min of foraging observations were compared with those gathered after the first min. Since no significant difference occurred ($P > 0.05, \chi^2$). the data were pooled.

I censused the densities of birds in the undisturbed fir forest, using a plot of 3.3 ha (8.3 acres) (Table 2). Eight counts of about 1 h were made in this area between 06:00 and 11:00 during the last 2 weeks of June 1977. If individuals held territories at the edge of a plot, I counted the number of observations made inside and outside of this plot and assigned the pair an appropriate fraction of total occupancy. Additionally, I made censuses of a plot in the same way at each of 3 sites at lower elevations; 950 m (second growth dominated by conifers), 850 m (second growth dominated by deciduous growth), and 750 m (tall mixed forest).

TABLE 2

DENSITY OF SMALL PASSERINE BIRDS ON STUDY SITE IN PAIRS/40 HA (100 ACRES)

	Census plot			
Species	Top (1150 m)	Next to top (950 m)	Next to bottom (850 m)	Bottom (750 m)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	–	22	30	–
Brown Creeper (*Certhia familiaris*)	–	–	–	12
Winter Wren (*Troglodytes troglodytes*)	–	9	9	–
Swainson's Thrush (*Catharus ustulatus*)	–	34	42	11
Gray-cheeked Thrush (*C. minimus*)	22	23	9	–
Ruby-crowned Kinglet (*Regulus calendula*)	–	10	–	–
Solitary Vireo (*Vireo solitarius*)	–	–	–	10
Red-eyed Vireo (*V. olivaceus*)	–	–	–	35
Nashville Warbler (*Vermivora ruficapilla*)	2	6	18	–
Magnolia Warbler (*Dendroica magnolia*)	–	57	–	–
Black-throated Blue Warbler (*D. caerulescens*)	–	–	–	20
Yellow-rumped Warbler (*D. coronata*)	31	12	–	–
Black-throated Green Warbler (*D. virens*)	–	–	–	50
Blackburnian Warbler (*D. fusca*)	–	–	–	21
Blackpoll Warbler (*D. striata*)	47	101	92	6
Ovenbird (*Seiurus aurocapillus*)	–	–	–	38
Canada Warbler (*Wilsonia canadensis*)	–	–	31	15
American Redstart (*Setophaga ruticilla*)	–	20	–	10
Purple Finch (*Carpodacus purpureus*)	–	12	–	–
Dark-eyed Junco (*Junco hyemalis*)	23	12	20	12
White-throated Sparrow (*Zonotrichia albicollis*)	23	25	–	–
TOTAL	148	342	252	238

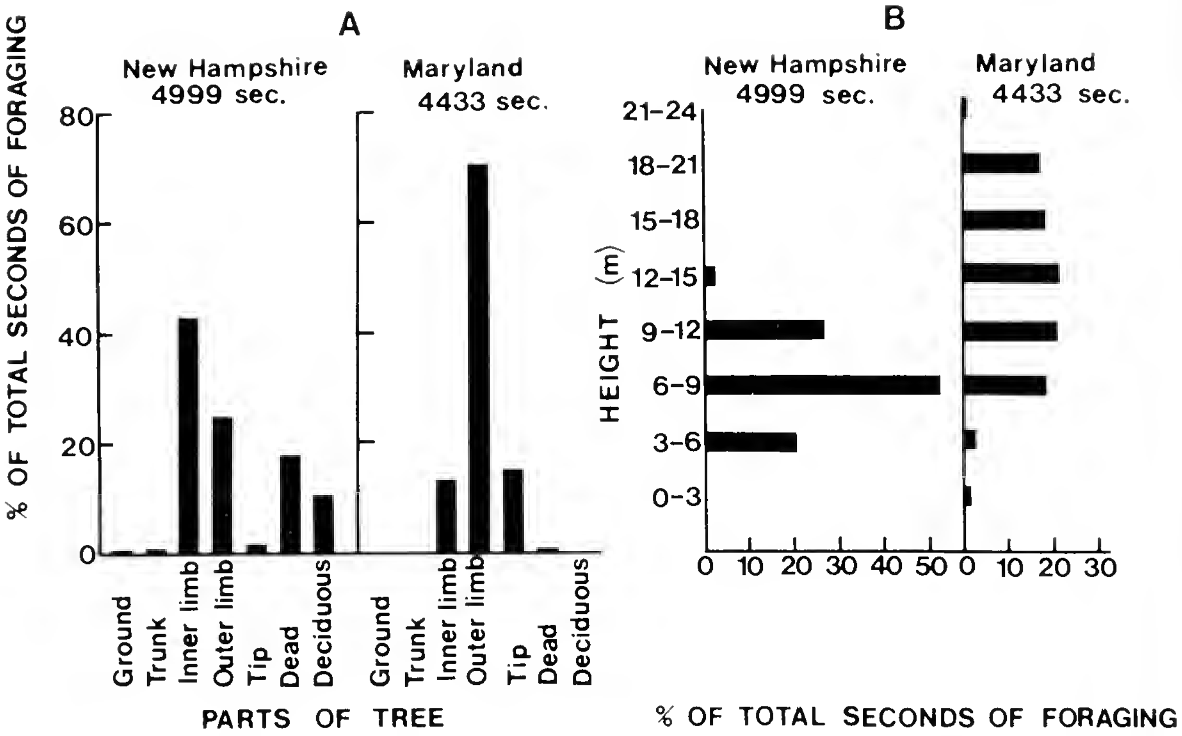

FIG. 2. Percentages of time spent foraging in different parts of tree; heights at which foraging took place.

RESULTS

Foraging observations on the breeding grounds.—Blackpoll Warblers usually foraged at medium heights in conifers, using the inner parts of the limbs most frequently. The heights foraged (Fig. 2) did not differ significantly from the profile of the forest (Fig. 1) ($P > 0.05$ in a 2-tailed Spearman Rank Correlation Test). In addition to the predominant foraging motion of gleaning, individuals occasionally hawked for insects and fed while hovering next to vegetation (Table 3). In the relatively few observations made on deciduous (white birch) foliage on the breeding grounds, Blackpoll Warblers showed a stronger tendency to forage on small outer parts of limbs than they did in the adjacent firs. In 40 foraging observations totalling 443 sec there, they foraged 32% of the time on the inner parts of limbs, 61% on the outer parts, 4% on tips of foliage, and 3% on dead limbs.

Blackpoll Warblers spent a considerable part of their time perching motionless or singing while perched motionless. In addition to the 4999 sec of foraging observations, 5288 sec were recorded in which individuals were stationary: therefore, foraging took up only 49% of the total time observed. These figures probably are conservative, since I frequently searched for

TABLE 3

FORAGING MOTIONS OTHER THAN GLEANING

Motion[1]	New Hampshire	Maryland
Hawking for insects	1.8 (9)	4.1 (18)
Hovering at vegetation	1.0 (5)	0.5 (2)
Retrieving fallen food	–	0.9 (4)

[1] Number/1000 sec of foraging, with total number of observations in parentheses.

considerable periods before locating singing birds. Probably I did not sight them sooner because they were not moving.

Foraging observations in migration.—All foraging in deciduous forests took place in the canopy. The heights exploited (Fig. 2) did not differ significantly from the foliage profile of the canopy (Fig. 1) ($P > 0.05$ in a 2-tailed Spearman Rank Correlation Test). Individuals foraged significantly more peripherally here than in the fir forests in New Hampshire ($P = 0.05$ in a 1-tailed test), but this difference probably resulted partly from differences in the location of foliage in deciduous and coniferous trees. The area treated as the inner parts of the branches here consisted of limbs of 3 cm diameter or more, which in Maryland typically did not support leaves, bark, or lichens that would be likely to provide hiding places for insects. However, a minority of the birds' time was also spent foraging in new leaf clusters, a pattern that did not parallel the one seen in the conifers. These birds hawked for insects somewhat more frequently than did individuals in the breeding area (Table 3), although the difference was not significant ($P > 0.05$, χ^2). These birds also occasionally hovered at the tips of vegetation (Table 3).

Intermittent observations were also made on Blackpoll Warblers during spring migration on several spruce-clad islands off the Maine Coast from 1966 to 1972. These observations were made on Thief, Crane and Franklin islands, which have a white spruce cover resembling the fir forest near the top of Mt. Osceola. Since a total of only 1101 sec of foraging observations was recorded on 3 islands of slightly differing foliage characteristics (see Morse 1971), a detailed comparison is inappropriate. However, here, too, Blackpoll Warblers made very heavy use of the inner parts of the limbs (64%) and only occasional use of the tips of the vegetation (4%). Individuals on these islands made minimal use of dead limbs (4%), which may be a function of the small number of dead limbs in the trees exploited on these islands. Neither did these individuals forage in deciduous growth, which could result solely from the virtual lack of deciduous trees on these islands. These birds concentrated their activities in the 6–9 m height category (79%), which is slightly higher than that recorded from Mt. Osceola (Fig. 1). However, this difference, too, may result from slight differences in the height of the forests on the islands and the upper parts of Mt. Osceola. In general, these migrants foraged very similarly to the breeding birds on Mt. Osceola.

Censuses on the breeding grounds.—In addition to their usually noted locations on mountain tops, Blackpoll Warblers occurred commonly down the mountainsides in largely second-growth habitats. In fact, their overall densities in these locations were as much as twice as high as those near the summit of Mt. Osceola (Table 2). However, they made up approximately the same proportion of the overall bird fauna at each of the top 3 study areas (30–36%), and the low density near the top correlates with a low overall density of birds (Table 2). Only in the lowest census area was the Blackpoll Warbler not the most abundant bird species (Table 2). It was the only warbler found in all 4 census plots. Among other warblers, only the Nashville Warbler (*Vermivora ruficapilla*) was found in 3 of the 4 plots.

DISCUSSION

Foraging patterns.—While marked differences in foraging exist between Blackpoll Warblers in coniferous and deciduous vegetation, they may not be as great as they appear at first glance. The difference in height seems to be a function of the height of the forest, with the birds in all situations concentrating their activities in the middle parts of the canopy, although they were seen at times in the top of the canopy in the deciduous forest in migration. While individuals concentrated their activities on the inner parts of the limbs on conifers and the outer parts on the deciduous trees. their position relative to the foliage was probably quite similar, as a result of the differences in leaf distribution in conifers and deciduous trees. In no situations did they frequently exploit the tips of the foliage. Foraging patterns of migrant and breeding individuals in conifers were very similar. Therefore, the impression gained in each area is one in which individuals concentrate their activities well in from the extremities of the vegetation and at modest heights.

These observations closely parallel those of Parnell (1969) in a number of habitats in North Carolina, where he found them typically to be birds of the mid-crown. Sick (1971) has also reported upon the habitat choices and foraging patterns of Blackpoll Warblers on their wintering grounds in Brazil. There, these birds made heavy use of tamarind trees (*Tamarindus indicus*), which superficially resemble conifers, by virtue of their needle-like leaflets.

In particular, blackpolls showed a strong tendency to exploit the shaded interior parts of these trees—similar to their exploitation of conifers.

Habitat distribution on the breeding grounds.—While the Blackpoll Warbler is often considered a mountaintop bird at the southern limit of its range (Griscom and Sprunt 1957), the altitudinal gradient of these birds on Mt. Osceola is high, with apparently breeding individuals ranging down to as low as 750 m, and with high densities being recorded as low as 850 m in second-growth vegetation. The altitudinal range of these birds on the mountain was greater than that of any other warbler and greater than that of any other species except the Dark-eyed Junco (*Junco hyemalis*) (Table 2). Able and Noon (1976) noted similarly wide gradients of Blackpoll Warblers in the Adirondack Mountains of New York and Green Mountains of Vermont.

Relationships with Bay-breasted Warblers.—Blackpoll and Bay-breasted warblers are very similar morphologically. Perhaps not generally appreciated is the fact that these 2 species apparently infrequently overlap in their breeding sites, although their composite geographic ranges show high degrees of overlap (Griscom and Sprunt 1957, AOU Check-list 1957). In New England, the Blackpoll Warbler is usually a species of relatively high elevations. The Bay-breasted Warbler, on the other hand, typically occurs at low elevations in spruce-fir forests and is associated with outbreaks of the spruce budworm (*Choristoneura fumiferana*) as well. Of the many breeding-bird censuses run in northern coniferous forest habitats (see Erskine 1971, 1972, 1976), Blackpoll and Bay-breasted warblers have been recorded together at the same site (several census plots) only in the Green River watershed of northern New Brunswick. Further investigation of the 2 species there would be profitable.

One possible explanation for this largely contiguous distributional pattern is that these species are too similar to each other to coexist. That interpretation is supported by the similarities in their foraging patterns (Morse 1978, this paper). Both concentrate their activities toward the centers of coniferous trees at moderate heights. The similarities in foraging patterns of these species are greater than those of any other members of the coexisting complex of *Dendroica* warblers (MacArthur 1958; Morse 1968, 1971). It is tempting to conclude that the boundaries of limiting similarity have been violated in this case. Although these species were studied in different forests with modestly differing foliage profiles, thus making a direct measurement of overlap impractical, the tendency of Blackpoll Warblers to shift their foraging height somewhat in response to the height of the canopy suggests that if they did occur with Bay-breasted Warblers at a site, they would exhibit a foraging pattern extremely similar to that species.

SUMMARY

Foraging patterns of Blackpoll Warblers were studied on their breeding grounds in mountain fir forests of New Hampshire and during migration in Maryland and Maine. Populations were also censused at several altitudes in New Hampshire. Blackpoll Warblers spent most of their time foraging on inner parts of vegetation at medium heights, although their placement in deciduous trees was more peripheral than that in conifers, probably a result of differences in the distribution of foliage. Blackpoll Warblers were the commonest species of bird in mountaintop fir forests, but their density there was lower than that found in some mixed coniferous-deciduous, second-growth areas on the mountainsides. They showed the widest altitudinal gradient of any warbler and a wider one than any other passerine except the Dark-eyed Junco.

Blackpoll Warblers forage very similarly to Bay-breasted Warblers, and only 1 of the 2 appears to breed at most sites. I suggest that their habitat use patterns are so similar that they cannot coexist under most circumstances.

ACKNOWLEDGMENT

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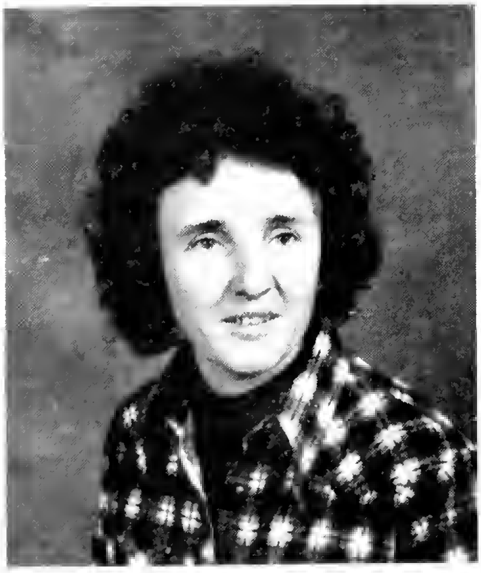
NEW LIFE MEMBER



Ms. Kathy Martin has become a life member of the Wilson Ornithological Society. Ms. Martin is presently conducting a research project on waterfowl as a part of the Dunk River Interdisciplinary Research Project. Her principal research interest is in population dynamics of upland game and passerine species. With a number of scientific and popular publications to her credit, Ms. Martin is also active in natural history and environmental organizations, recently serving as representative from P.E.I. to the Canadian Environmental Advisory Council Conference. In addition to her ornithological interests, Ms. Martin enjoys scuba diving, writing, photography, and is active in a variety of sports.

Wilson Bull., 91(2), 1979, pp. 244–254

FORAGING ECOLOGY OF STRICKLAND'S WOODPECKER IN ARIZONA

Hans Winkler

Davis (1965) was the first to shed light on many problems regarding the systematics, morphology, and ecology of Strickland's Woodpecker (*Picoides stricklandi*). Drawing arguments from all these fields he showed that the forms with plain backs and those with barred backs are similar enough to each other to be considered 1 species. The northern populations of the "*arizonae*" form of the species (those from Arizona, NW Mexico, N Sinaloa, S Sinaloa, Nayarit, W Michoacán, Tzitzio-Las Trojes), according to him, differ ecologically more from southern "*arizonae*" populations than all of these differ from "*stricklandi*" (México, Veracruz) populations. The woodpeckers of northern Mexico, Arizona, and New Mexico seem to prefer oaks as feeding stations whereas the other populations live in pine forests (Davis 1965). The birds of the Chiricahua Mountains belong to the populations which are believed to prefer oaks (see Davis 1965). Balda (1967) found only a few Strickland's Woodpeckers in his oak woodland study area in the Chiricahua Mountains. He recorded more in the oak-juniper woodland and in the riparian canyon both of which contain some pines (mainly Apache pine [*Pinus engelmannii*] and Chihuahua pine [*P. leiophylla*]). Ligon (1968 a,b) made observations both on "*stricklandi*" and "*arizonae*" and confirmed Davis' findings on ecology. He also found ecological differences between the sexes in these woodpeckers that parallel morphological differences. In "*stricklandi*" the sexes differed predominantly in the selection of different portions of the trees and in "*arizonae*" they differed mainly in methods of foraging (Ligon 1968a). However, the data (Ligon 1968b) seem to me not totally convincing in this respect. In both cases, males, which have the longer bills, appeared to prefer the lower regions of a tree, i.e., the trunk.

Various studies on other species of *Picoides* showed that marked differences in feeding behavior due to different ecological situations might occur (Austin 1976; Hogstad 1976; Jackson 1970; Skoczylas 1961; Travis 1977; Winkler 1972, 1973; for a general discussion of the problems involved see Curio 1975). Davis (1965) indicates that shifts can also be found in the Strickland's Woodpecker's feeding behavior. Because of the importance of such studies in ecological comparisons (Selander 1965), I provide here further evidence of variation in the behavioral ecology of this species.

METHODS

My studies were carried out in the Chiricahua Mountains, Cochise Co., Arizona, in some of the same areas where Ligon and Davis worked. The main habitat investigated was the riparian woodland along the South Fork of Cave Creek Canyon down to the Portal Ranger Station. Other observations were made in the woodland around the Southwestern Research Station of the American Museum of Natural History. I observed the woodpeckers from 12 March to 6 May 1974 (excepting 14–18 April). Ecological data were obtained by walking slowly and irregularly through the habitats. For the analysis of feeding techniques and feeding strata I included only what the bird was doing when I first encountered it. I followed a bird as long as the bird showed no signs of alarm, or until I lost contact with it. As in previous studies (Winkler 1973), I rejected from analyses foraging data obtained within 1 h before sunset, data from encounters that resulted from my having heard the bird pecking, and data on feeding activities occurring during or closely after interactions with other Strickland's Woodpeckers. Data edited in this way should be statistically reliable. In order to get estimates of the various activities of the woodpeckers for estimates of a time budget, I determined the relative frequencies of 5 min intervals in which a particular activity was recorded at least once. A total of 2907 intervals (practically the entire time spent in woodpecker occupied areas) served as a basis for these estimations, the assumption being that my method of observation (including observations at trees with holes) did not systematically influence the data (a safe assumption at least for the very far reaching signals).

At least 5 pairs of Strickland's Woodpeckers were observed. At first I analyzed data by 10-day periods, though statistical analysis justified lumping ecological data into 2 seasonal subunits: (1) the period between 12 March and 20 April, and (2) the period from 21 April to 6 May.

RESULTS

Fig. 1 gives the proportion of tree species used by male and female Strickland's Woodpeckers in the riparian canyon. Only those observations that showed the woodpeckers pecking were considered. Thus possible distortion resulting from the use of all feeding techniques was excluded. Considering Balda's (1967) data on the plant species composition and these findings, it is readily seen that both sexes preferred pines during the first seasonal segment. Through application of coefficients of selection (Jacobs 1974) it appears that during the nesting season (21 April to 6 May), males used pines roughly in proportion to their abundance (the same is true when comparing frequencies) and preferentially used Arizona sycamores (*Platanus wrightii*) in both seasonal subunits particularly the later one. Females used pines slightly more than males in both seasonal divisions. Neither sex preferentially used oaks as a pecking substrate, but rather, seemed to avoid them. Differences between the sexes ($\chi^2 = 5.560$, $N = 79$) were not significant during the first period. They are significant in the second of the 10-day periods ($\chi^2 = 10.965$, $P < 0.05$, $N = 25$). However, if the records of males on sycamores are lumped with the category "other trees,"

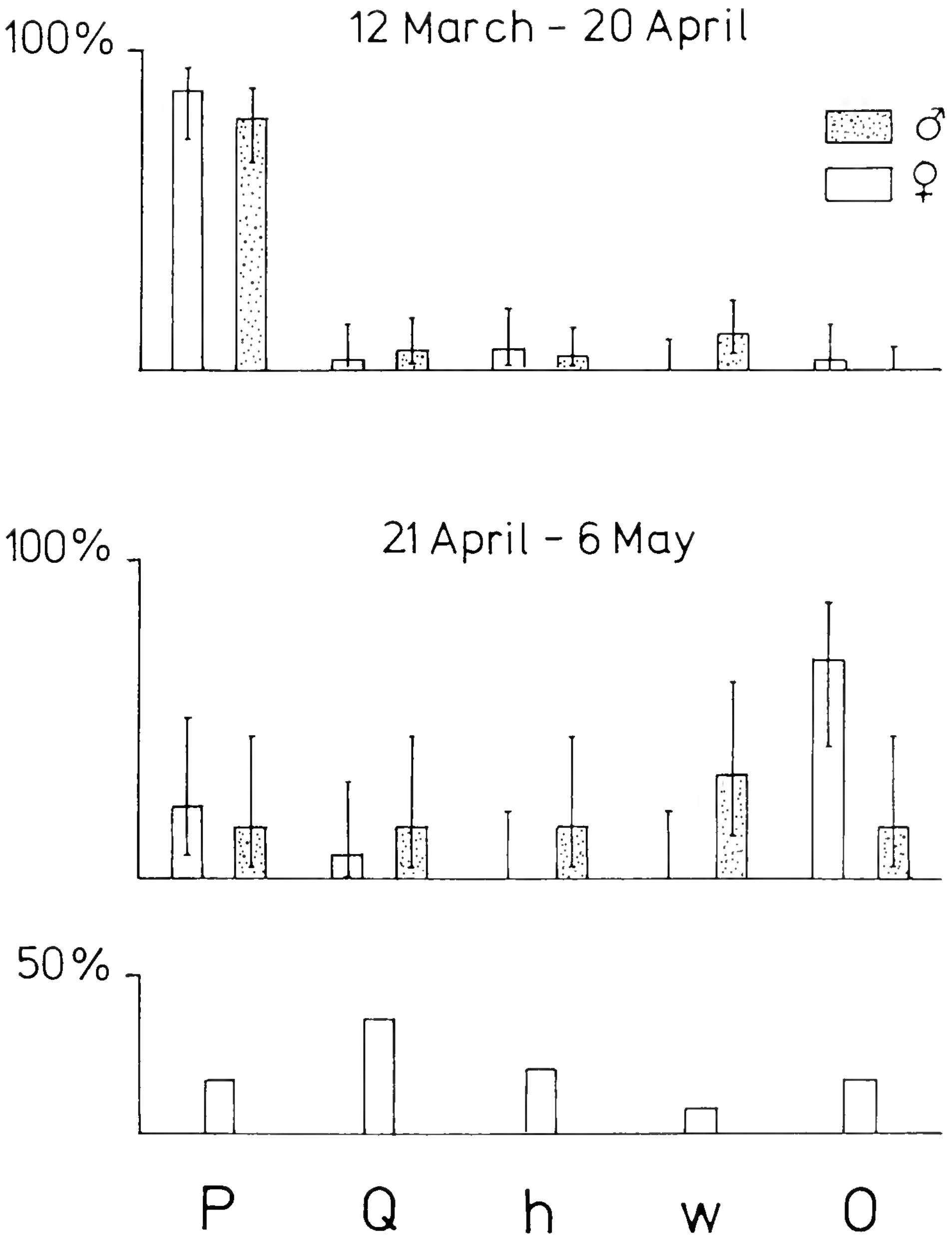


FIG. 1. Proportion (with 95% confidence limits) of tree species used by female (N = 32, 13) and male (N = 47, 12) Strickland's Woodpeckers. The relative density values of the corresponding tree species are shown in the bottom row based on data from Balda (1967).

P: Apache pine (*Pinus engelmannii*), Chihuahua pine (*P. leiophylla*), and ponderosa pine (*P. ponderosa*) combined. Q: three oak species (*Quercus arizonica*, *Q. rugosa*, and *Q. emoryi*) combined. h: Silverleaf oak (*Q. hypoleucoides*). w: Arizona sycamore (*Plantanus wrightii*). O: other trees including agave *Agave* sp. and alligator juniper (*Juniperus deppeana*). All data from the South Fork of Cave Creek Canyon, Chiricahua Mts., Arizona.

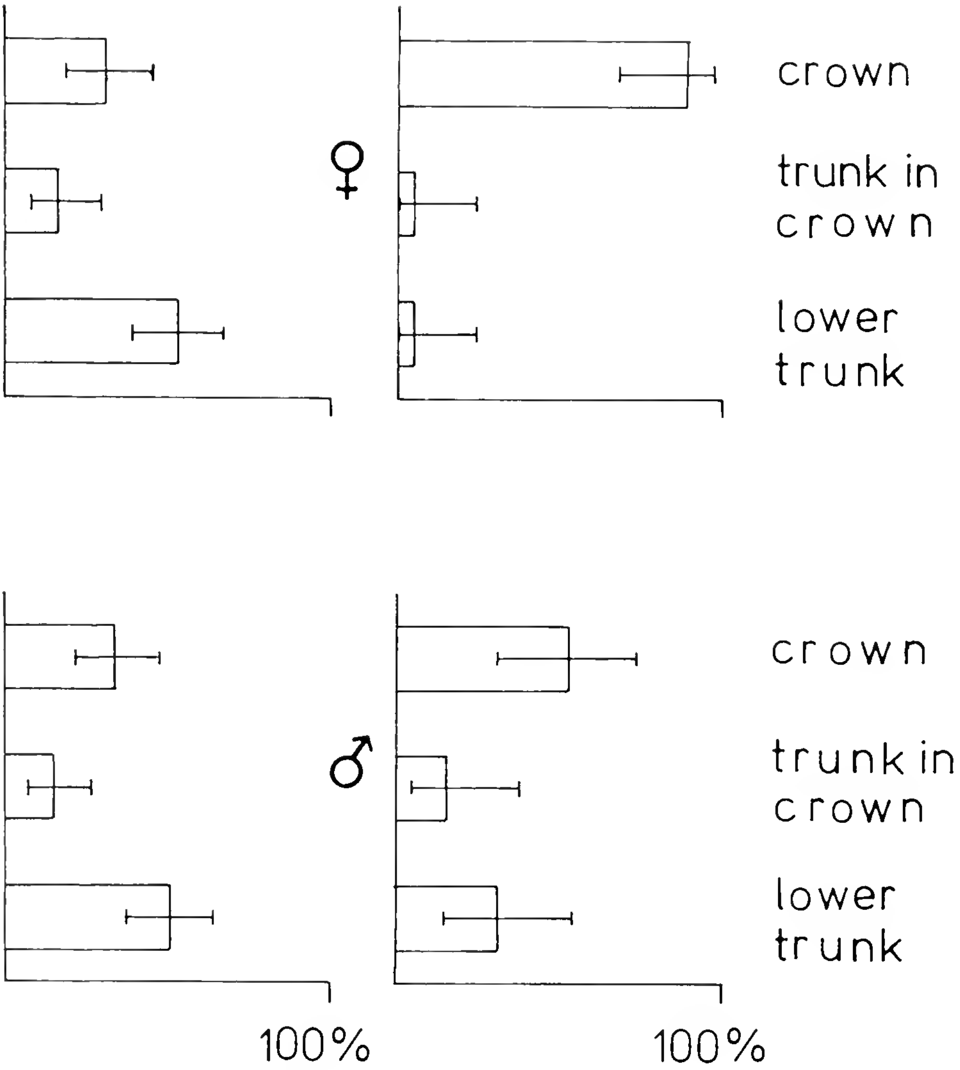


FIG. 2. Relative use (with 95% confidence limits) of the parts of a tree by female (N = 49, 16) and male (N = 59, 19) Strickland's Woodpeckers. Data from the first seasonal period (12 March–20 April) are given on the left and from the second one (21 April–6 May) on the right.

these differences disappear. In the last week 2 females were almost always found in 1 dead Douglas-fir (*Pseudotsuga menziesii*) and these might bias the data considerably (also those in the sections below). Differences between the seasons for females were significant ($\chi^2 = 24.995$, $P < 0.005$, $N = 45$) and for males ($\chi^2 = 19.995$, $P < 0.001$, $N = 59$).

Silverleaf oaks (*Quercus hypoleucoides*) have a smooth bark whereas the other oaks (*Q. arizonica*, *Q. rugosa*, *Q. emoryi*) have a rough furrowed bark and therefore were separated in the analysis. The woodpeckers only hammered vigorously on silverleaf oaks.

To facilitate further analysis of foraging (all activities) 3 subdivisions of a tree were recognized: trunk below crown, trunk within crown, and the crown. There were only a few observations of woodpeckers feeding on dead limbs lying on the ground or feeding on agave and these observations were not included in these analyses. While males and females did not differ in their use of foraging sites during the first seasonal period (Fig. 2), during the second period females foraged significantly more in the crowns than did males ($\chi^2 = 5.018$, $P < 0.05$, $N = 35$). The seasonal shift shown by females is significant ($\chi^2 = 15.996$, $P < 0.0005$, $N = 65$), and while that shown by males is not significant, a similar trend toward foraging more in the crown is apparent.

Three main methods of obtaining food were recognized: gleaning, probing, and pecking. Characteristically this species (and the Hairy Woodpecker [*P. villosus*], Kingsbury 1932, pers. obs.) excavates narrow, deep holes and subsequently probes them for food. This behavior was included in the pecking category. Not analyzed were the light taps used when searching bark surfaces as well as other searching activities.

I found no sexual differences, or seasonal shifts in foraging techniques used by this species (Fig. 3). Pecking was the most commonly used technique.

Seasonal shifts in foraging sites could also be associated with other activities (Fig. 4). Females seem to be affected more; e.g., they spent 1.2 times more in nesting activities than did males. It appeared that as nesting time approached, the time spent in feeding activities became less. I first observed incubating birds on 27 April.

As a further indication of a possible interaction between signalling and foraging behavior, it should be briefly mentioned that also such an activity as acoustic behavior is "stratified." Both males and females gave 75% of their rattles (66 analyzed) and 60% of their call notes (70 analyzed) in the crown. I found that 74.3% of the drumming (40 analyzed) was also performed in the crown.

DISCUSSION

The data presented here show that the woodpeckers change their foraging habits in conjunction with internal and external changes. This relates to the problem of generalists vs. specialists. In short (Alcock 1975, Curio 1975, Morse 1971), "generalist" feeding should occur during food shortage and "specialist" feeding during high prey availability, but this seems to be in contrast to the findings of this as well as other studies (Curio 1975). The designations "specialist" or "generalist," respectively, indicate according to Morse (1971) whether an individual "concentrates the majority of its activities on one or a few categories" or whether it uses "several

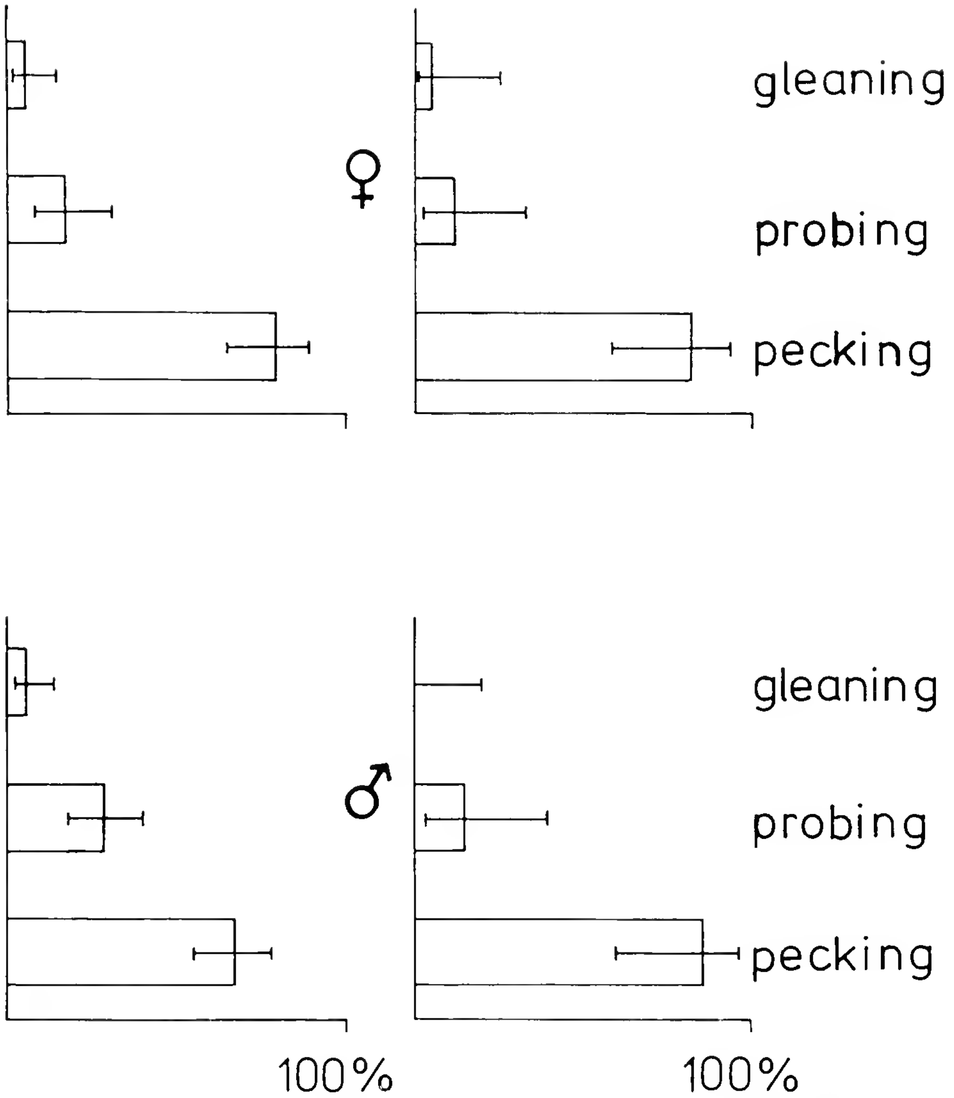


FIG. 3. Relative frequency (with 95% confidence limits) of the feeding techniques employed by female (N = 42, 17) and male (N = 72, 14) Strickland's Woodpeckers. Data from the first seasonal period (12 March–20 April) on the left and from the second one on the right (21 April–6 May).

categories with considerable frequency." One approach to this problem is to look at the possible behaviorial mechanisms and strategies underlying these categories. Two such strategies may be discerned. The first one I would call "schematic feeding," schematic because the behavioral elements exhibit low diversity, because they often are stereotyped (fixed action patterns), and because their interplay is quite fixed. Morphological features connected with this behavior are often regarded as highly specialized and well adapted. These traits, then, correspond to an environmental situation that provides predictable, though very often sparse, resources that have to be exploited efficiently.

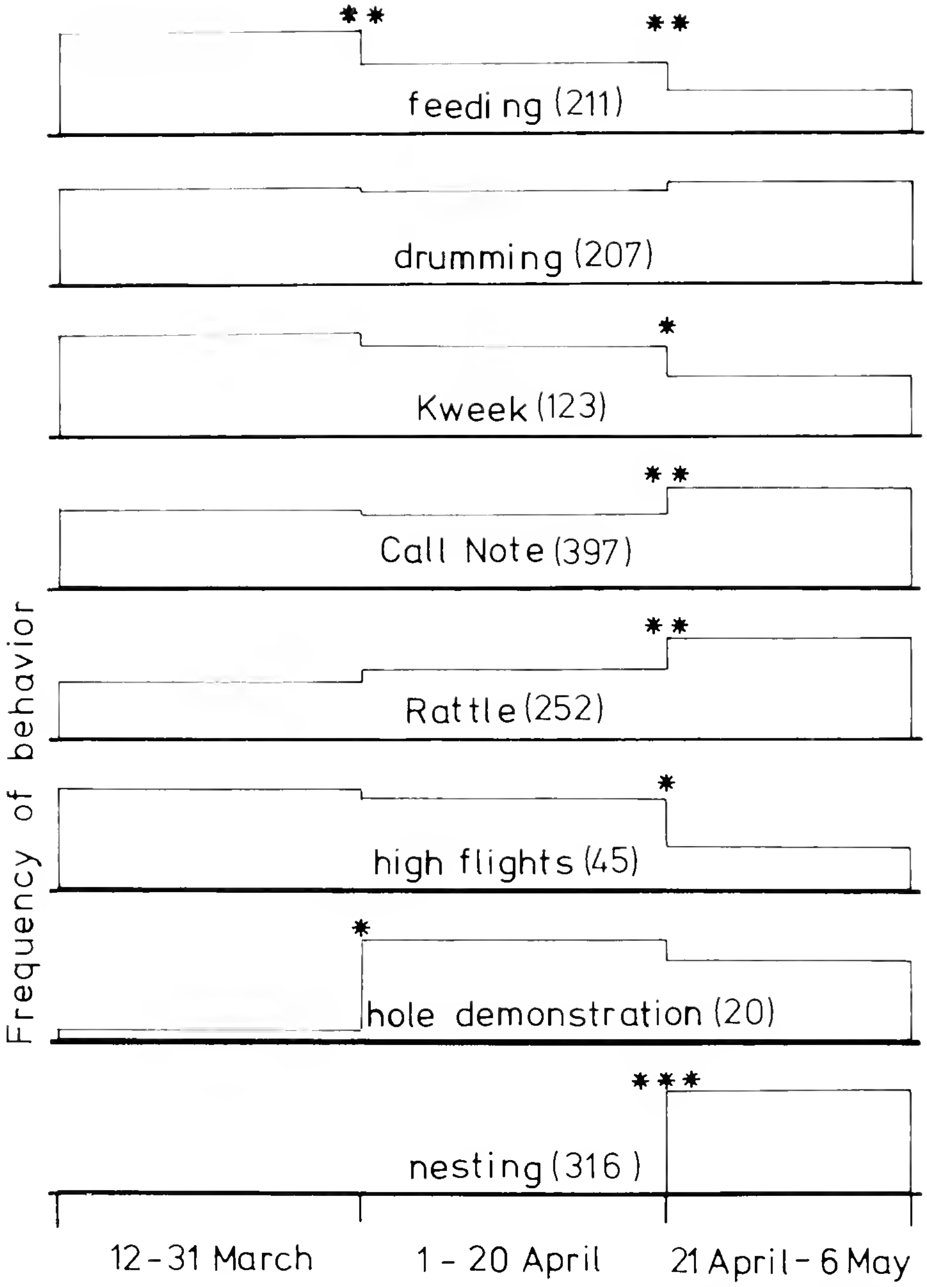


FIG. 4. Seasonal shifts in frequency of some behavior of Strickland's Woodpeckers. Drumming is a signal given by males; *kweek* is a call of females; call notes and rattles are vocalizations used by both sexes. "High flights" denotes long distance flights well above the tree tops. Hole demonstration behavior is a combination of visual and acoustical signals used by the birds for announcing prospective nesting holes. Asterisks denote the 0.05(*), 0.01(**), and 0.001(***) significance levels for the differences between adjoining periods (χ^2, based on the frequency of 5 min intervals in which the respective activity was recorded, see text). For the sake of better illustration, data were scaled after the largest section of each category. Total frequencies are given in brackets.

The second strategy shall be designated as "opportunistic feeding." Here behavior is diverse, hence more difficult to predict. The low adaptiveness of some techniques and associated morphological structures (like flycatching in pied woodpeckers, *Picoides*) can only be compensated for by a high availability of prey with high energy yield. This set of responses is associated with an environment that provides rich but temporally variable food supplies.

The general strategy is to switch or grade opportunistically from one of these substrategies to another. One would expect that specialized feeding is associated with schematic feeding. In general this is true, but specialized feeding is not exclusively confined to that category, hence, the aforementioned contradiction between data and theory. To become a "generalist" or to switch to opportunistic feeding has its costs, and it does not always pay; it obviously would be a waste of time for a woodpecker to sit in a tree top in winter waiting for the chance to flycatch a large insect.

Within opportunistic feeding, in accordance with present theory, temporally and locally high specialization for one, very abundant food source can be found, but taken over a longer period of time (see Winkler 1972), over a wider area and over more individuals, a generalistic pattern emerges. Furthermore opportunistic individuals should generalize temporally and locally if demand is high or supply is low as long as this strategy yields a payoff. Thus the apparent difficulties can be resolved by acknowledging the duality in the meaning of "specialist."

Previous studies of pied woodpeckers (Winkler 1973) showed that during the pre-nesting season conditions favoring schematic feeding are prevalent. This seems true for Strickland's Woodpecker as well. The data also show that the increase of opportunistic behavior is stepwise. Tree selection was affected first; males and females showed equally marked shifts. Stratum selection changed less drastically and more in females, who seemed to be under more stress, than in males. Therefore one can conclude that stratum selection is more conservative than tree species selection. Finally, the feeding techniques were unaffected. They may become affected, however, when the nesting season proceeds and the necessity for opportunistic feeding further increases. Data from other woodpeckers and also the observations of Davis (1965) and Ligon (1968a) support this assumption for Strickland's Woodpecker. These concepts are illustrated in Fig. 5.

Differences between the sexes seem to arise in *P. stricklandi* (not, for instance, in the Downy Woodpecker [*P. pubescens*], pers. obs.) during the time of opportunistic feeding only. Conclusions are thus difficult to draw; the very nature of opportunistic feeding, as it is thought of here, may give rise to a strong bias resulting from the feeding habits of individual birds in particular situations. Both Davis (1965) and Ligon (1968b) made

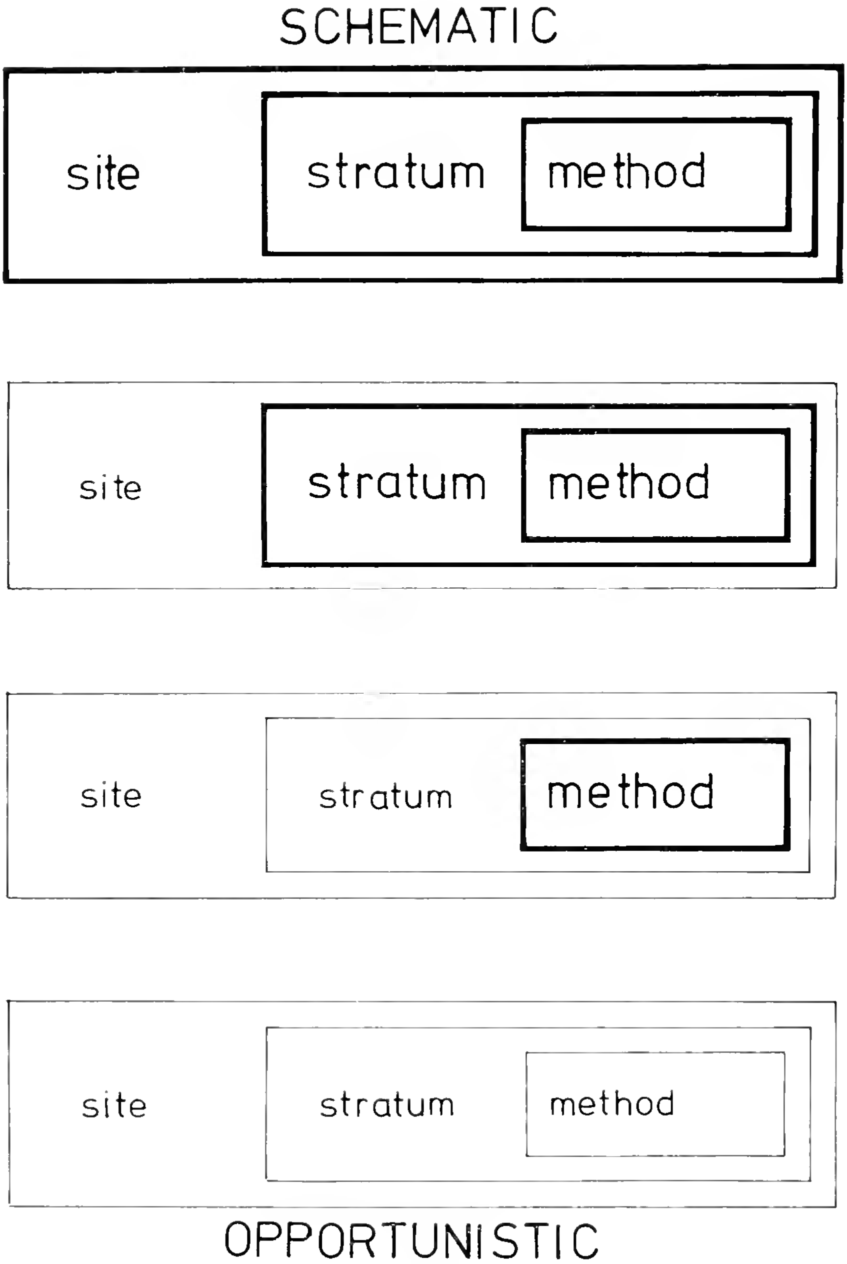


FIG. 5. Schematic representation of the differential effects of increasing opportunistic feeding behavior on site (here: tree species) selection, stratum selection, and feeding techniques. Dark lines and large letters indicate that the corresponding aspect of foraging behavior is fixed and restricted in variability.

their observations in Arizona in a season when opportunistic feeding should be prevalent (June and July, and May to July, respectively).

The characteristics of conservative schematic feedings are useful for many comparative studies and might even clarify evolutionary relationships. The previously unknown strong predilection for pines of even the northern populations of Strickland's Woodpecker fits well with the data for other populations (Davis 1965, Ligon 1968a). It also suggests that this species has evolved in a Mexican, pine-dominated, Pleistocene arboreal center. As the range of the Red-cockaded Woodpecker (*Picoides borealis*) is associated with that of loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) (Jackson 1971), so the range of the Strickland's Woodpecker is strikingly well associated with that of the Chihuahua pine (*P. leiophylla*) and Apache pine (*P. engelmannii*) (Mirov 1967). Hairy Woodpeckers also have some preference for pines in many areas (see Jackson 1971) and select them even in almost pure deciduous woodland (pers. obs.). The Mexican Chickadee (*Parus sclateri*) and the Mexican Junco (*Junco phaeonotus*) similarly seem to be confined to areas in which Apache and Chihuahua pines occur (Balda 1967). Grace's Warbler (*Dendroica graciae*) and the Yellow-throated Warbler (*D. dominica*), which can be found at the same localities as Strickland's Woodpecker and Red-cockaded Woodpecker, respectively (pers. obs.), may have had a similar speciation history (Mengel 1964) as these woodpeckers. The ecological data presented here are consistent with the hypothesis that Strickland's Woodpecker (and maybe the Red-cockaded Woodpecker, Jackson 1971) may have split off from an ancestral Hairy Woodpecker stock.

SUMMARY

Strickland's Woodpeckers were studied in the pre-nesting and early nesting periods in the Chiricahua Mountains of Arizona. This woodpecker prefers to feed upon pines in the pre-nesting season, but is less selective during the nesting season. In contrast to earlier reports, an avoidance of, rather than a preference for oaks was found. During the pre-nesting season, trunk feeding prevails; a preference for crown feeding emerges later. The relative frequency of use of various feeding techniques did not change during the period investigated. Changes in feeding behavior were associated with changes in other behavior. Differences between the sexes appeared only in the nesting season. Also, females differed from males with regard to patterns of seasonal change in behavior other than feeding. The changes in feeding behavior are discussed and the concept of schematic and opportunistic feeding is introduced.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to all the people who provided help with this study. Particularly I should like to mention L. L. Short who initiated my work with this woodpecker, V. Roth of the Southwestern Research Station, and my wife Thesi who assisted in some of the fieldwork. J. A. Jackson and J. Tate, Jr. made helpful comments about the manuscript. Generous financial support came from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, New York.

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THE ONTOGENY AND ORGANIZATION OF COMFORT BEHAVIOR IN ADÉLIE PENGUINS

Marc Bekoff, David G. Ainley and Anne Bekoff

Comfort behavior, which has been analyzed in detail in a variety of bird species (Kortlandt 1940; van Iersel and Bol 1958; McKinney 1965; Delius 1969; Ainley 1970, 1974; Borchelt 1975; van Rhijn 1977), serves an important function in maintenance of the body surface. Although many other aspects of avian behaviorial ontogeny have been studied extensively (e.g., prenatal motility, imprinting, song, caregiver–young interactions) much less is known about the development of comfort activities (Bekoff 1978). We studied the comfort behavior of Adélie Penguins (*Pygoscelis adéliae*) in order to answer, with a quantitative base, the following questions. (1) At what ages do various comfort movements first appear? (2) How do these behaviors become organized into sequences during ontogeny and later life? (3) In what ways (frequency, distribution, serial order) is the behavior of chicks different from the behavior of adults? Specifically, we were interested in analyzing processes of development to study the continuity of change from early ontogeny to adulthood. Comfort activities are a good behavioral phenotype for this kind of analysis because they appear early in life, are readily identified as individual acts that change little (if at all) in appearance during ontogeny (Thompson 1974, Spurr 1975, this study), and are repeated often. Adélie Penguins were particularly suitable for such a study because, while there is little known about the development of behavior in this species other than some general descriptions provided by Taylor (1962), Penney (1968), Thompson (1974) and Spurr (1975), the chicks are easily observable at all stages due to the simple ground nests built by the adults (Fig. 1a).

METHODS

Penguin chicks of known age (dye-marked offspring of banded adults) and adults (over 2 years of age) were studied at Cape Crozier, Ross Island, Antarctica, during the austral summer, 1974–75. Chicks were observed from hatching until the last week of January, shortly before fledging. Observations were made directly at close range or with the aid of binoculars. Behavioral sequences and a time indication (every 15 sec) were read directly into a cassette tape recorder and later transcribed. Since wind conditions may affect the performance of some comfort movements (Ainley 1974), all observations were made when winds were light.

We observed behavior sequences in the following 6 different groups of dry birds which had been out of the water at least 1–2 h prior to observation: (1) adults non-oiling (bill contact with the uropygial, or oil, gland was not made); (2) adults dry-oiling (contact

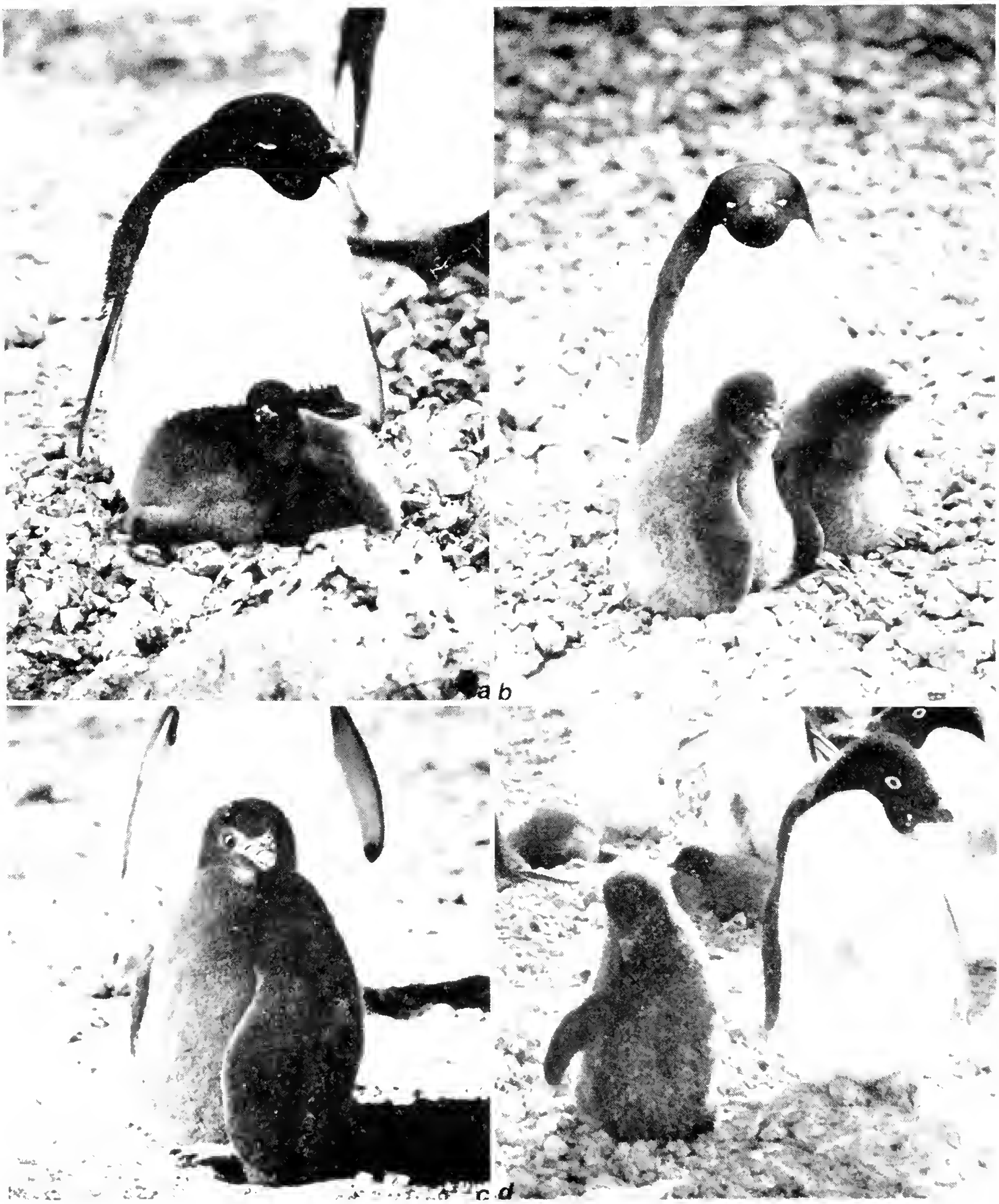

FIG. 1. (a) One-week-old chicks. Note the simple nest made of pebbles that surrounds the chicks and parent. (b) Two-week-old chicks. (c) Three- to 4-week-old chick. (d) Four- to 5-week-old chick preening its shoulder.

with the uropygial gland was made and oil was distributed over the dry plumage); (3) chicks aged 7–13 days (Fig. 1b) (4) 14–20 days (Fig. 1c), and (5) 21–28 days (Figs. 1d and 2a) non-oiling; and (6) chicks aged 35–43 days (Fig. 2c) dry-oiling (no dry-oiling was observed prior to 35 days of age).

Due to a number of factors (e.g., mortality, inactivity, weather conditions), it was not

FIG. 2. (a) Four- to 5-week-old chick back preening. Note the loose down. (b) Five-week-old chick preening its shoulder. (c) Six-week-old chick preening its shoulder. Note the patches of contour feathers on the breast, belly and wing. (d) Seven-week-old chick performing bill-to-wing-edge, during which the bird grasps the top edge of the wing between its mandibles and draws the bill along the wing's edge toward its body. This is the first step in the transfer of oil to the head.

possible to observe the same chicks or adults throughout the duration of the study so for analysis we assumed that the samples were independent.

Sequence analysis.—In order to compare series of comfort movements that differed greatly in duration, we used Ainley's (1974: 18–19) method to study behavioral sequences and temporal distribution of individual movements. To analyze 2-act transitions, data for some of the comfort movements were cast into 15 × 15 contingency tables (see Ainley 1974, Table 2 for the way in which comfort movements were combined). Z scores were calculated to determine whether the 2-act transition in each cell was significant (i.e., not random). This method has been used by several workers (Ainley 1974; Poole and Fish 1975, 1976; Stevenson and Poole 1976). In our analyses, we considered transitions between an act and itself (separated by a brief pause during which the bird lifted its head away from the body surface), although some workers have excluded them (e.g., Fentress 1972). We included these because they occur with a high frequency and simply are representative of what the animals did.

Actions observed.—The actions observed are listed in Table 1. Terminology and detailed

TABLE 1

LIST OF ACTIONS (AND CODE) OBSERVED AND DAY OF FIRST OCCURRENCE

Action*	Day	Action*	Day
Yawn (Y)	1	Rapid-wing-flap leading to Phase II wing-stretch	14
Head-shake (HS)	2	Wing-shake (WSh) (L,R,B)	15
Leg stretch (LS) (L,R,B)	6	Bill-to-wing-edge (BW) (L,R)	16
Rapid/slow-wing-flap (RWF, SWF)** (L,R,B)	6	Shoulder-rub (SR) (L,R)	33
Sneeze (SN)	6	Oil (L,R)	35
Wing-extend (WE) (L,R,B)	7	Preening (L,R):	
Nibble-preen of various body regions	7	Breast (BR)	7
Wing rub (WR) (L,R)	7	Belly	7
Phase II wing-stretch (PII)	9	Back	9
Tail-wag (TW)	9	Side	10
Ruffle-shake (RS)	9	Wing	12
Bite-wing (BWg) (L,R)	9	Shoulder (SH)	13
Foot-shake (FS)	10	Leg	14
Wing-stretch with yawn (WSY)*** (L,R,B)	12	Cloaca (CL)	15
Wing-stretch (both with body shake) (WSBS)	13	Flank	15
Head-scratch (HSC) (L,R)	14	Tail-base (TB)	21

* For full descriptions see Ainley (1974) and text. L = left, R = right, B = both left and right. The following actions were not observed in chicks: body-shake (BS), neck-stretch (NS), ruffle-feathers only (RF).

** The mean rate of rapid-wing-flapping for adults (N = 27) was 5.5 cycles/sec and that for chicks (N = 18) was 3.7 cycles/sec (determined by movie analysis, $t = 2.12$, $df = 43$, $P < 0.05$).

*** Can occur without yawn.

descriptions provided by Ainley (1970, 1974) are used throughout. See Figs. 1, 2 and 3 for photographs of chicks of different ages and an adult performing some of the common comfort actions.

RESULTS

Age at first performance of comfort movements.—Prior to day 7 when 4 new actions were recorded, 5 actions had been observed (Table 1). By day 21, all actions except "shoulder-rub" (SR) and "oil" had been observed. Our data on the first occurrence of preening directed to various parts of the body surface agree with those of Spurr (1975, pers. comm.).

No oiling was observed prior to 35 days. We noted that chicks began to exude oil from the uropygial gland between 30–33 days of age: none of the 8 chicks checked were secreting oil prior to day 30. After day 33, all of the 11 chicks checked were secreting oil. The feather tuft extending out of

FIG. 3. Wing-rubbing by an adult. This is the action used to transfer oil from the wing edge (Fig. 2d) to the head. Note the feather tuft surrounding the uropygial gland at the base of the tail.

the gland (Fig. 3) did not reach full length until days 31–38. When oiling, the penguins contact this tuft with the bill.

The growth of contour feathers may have a great deal to do with the appearance of several behavior patterns (see Discussion). By day 17, feather sheaths were visible amidst the down and there was a lot of loose down. By day 20, small contour feathers were observable on most chicks. Taylor (1962) and Spurr (1975) also observed that loss of down began at approximately 3 weeks of age.

TABLE 2

A. THE MEAN DURATION (MIN) AND B. THE MEAN RATE (ACTS PER MIN) FOR NON-OILING AND DRY-OILING SEQUENCES BY CHICKS AND ADULTS

Non-oil sequences				Dry-oil sequences	
Chicks			Adults	Chicks	Adults
Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6
A. Mean duration[1]					
0.6 (N = 12)	6.3 (N = 15)	8.4 (N = 7)	7.1 (N = 26)	16.5 (N = 6)	9.4 (N = 1)
(SD = 1.7)	(2.7)	(3.5)	(4.6)	(8.1)	(8.7)
B. Mean number of acts/min[2]					
3.3	4.5	4.7	6.2	6.9	8.5
(0.9)	(1.2)	(1.4)	(2.1)	(1.6)	(2.5)

[1] When all 6 groups were compared (one way analysis of variance: $F = 4.69$, $df_1 = 5$, $df_2 = 76$, $P < 0.001$) only 7–13-day chick non-oiling sequences (group 1) and chick dry-oiling sequences (group 5) differed in mean duration (Duncan's Multiple Range Test). (When the largest variance was more than 1.5 times greater than the smallest variance, a log transform was used.)

[2] When all 6 groups were compared ($F = 6.32$, $df_1 = 5$, $df_2 = 76$, $P < 0.001$), it was found that group 2 did not differ significantly from group 3 and group 4 did not differ from group 5.

Comfort sequence analyses

The mean duration (min) of comfort sequences is presented in Table 2a. The duration of non-oiling sequences did not differ when 14–20-day chicks, 21–28-day chicks and adults were compared. However, 7–13-day chicks performed significantly shorter non-oiling sequences than those of older chicks and adults and the first dry-oiling sequences by chicks 35–43 days of age were significantly longer than those of adults.

The mean number of acts performed per min (rate) is presented in Table 2b. Adults performed comfort behavior actions at significantly higher rates than did chicks when the same types of comfort sequences were compared. Since the durations of non-oiling sequences in chicks were about the same as (14–20 days; 21–28 days) or shorter than (7–13 days) in adults and the rate was lower in chicks, fewer acts were performed per non-oiling sequence in chicks. However, we observed a gradual increase with age in the mean number of acts performed per non-oiling sequence. The mean number of times oiling was performed in dry-oiling sequences also increased from 4.7 in 35–43-day chicks to 6.2 in adults.

Distribution of comfort movements

Frequency of occurrence.—The frequency with which 10 comfort actions occurred was compared for chicks and adults. These frequencies were

TABLE 3

THE DISTRIBUTION IN TERMS OF RELATIVE % OF OCCURRENCE OF 10 COMFORT ACTIVITIES DURING NON-OILING AND DRY-OILING SEQUENCES BY CHICKS AND ADULTS[1]

	Non-oiling sequences				Dry-oiling sequences		
	Chicks			Adults	Chicks	Adults	
Behavior	Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6	Proportions[2] test
Oil	–	–	–	–	3.7	9.1	
Bill-to-wing-edge	–	1.0	0.8	4.8	2.6	5.0	2 = 3, 4 = 6
Wing-rub	8.2	4.9	3.7	13.8	4.8	14.3	2 = 3, 2 = 5, 3 = 5
Shoulder-rub	–	–	–	11.4	12.9	9.8	4 = 6
Preen breast	30.0	21.6	24.8	15.9	12.0	13.6	2 = 3, 4 = 6, 5 = 6
Preen back	12.2	9.8	5.4	5.8	16.0	5.2	3 = 4, 3 = 6, 4 = 6
Preen side/flank	6.1	9.4	8.6	13.6	12.1	14.7	2 = 3, 4 = 5
Preen leg	1.7	3.6	8.8	1.5	6.1	2.2	1 = 4, 1 = 6, 4 = 6
Preen belly	11.7	7.2	7.4	3.6	5.6	4.8	2 = 3, 4 = 6, 5 = 6
Ruffle-shake	1.7	1.2	2.8	0.9	–	0.5	1 = 2, 4 = 6

[1] See Table 2 for sample sizes.

[2] Results of a proportions test. An "=" sign means the groups did not significantly differ from one another ($Z < \pm 1.96$, $P > 0.05$).

expressed as a percentage derived from the number of times a particular act occurred out of the total number of acts performed in a sequence (Table 3). Several differences and trends were identified. (1) The most frequently observed comfort act in chicks was breast preening, as was also true of the tern (*Sterna* spp.) chicks observed by van Iersel and Bol (1958). (2) There was a general trend toward a decrease in breast preening with increasing age (except at 21–28 days) during non-oiling. However, there was no difference in the relative frequency of breast preening when dry-oiling by chicks (35–43 days) and adults were compared. (3) Back preening (Fig. 2a) during non-oiling generally declined as the chicks grew older until, by 21–28 days, the same relative frequency as in adults was seen. The highest relative frequency of back preening was seen in 35–43-day chicks during dry-oiling. (4) Belly preening occurred more frequently in chicks than in adults during non-oiling, but at similar frequencies during dry-oiling. (5) While breast, back and belly preening tended to decrease with age, side and flank preening during non-oiling increased. Side and flank preening also occurred more frequently during dry-oiling by adults than chicks. (6) During dry-oiling, chicks performed oiling, bill-to-wing-edge (Fig. 2d) and wing-rub (Fig. 3), 3 behaviors which are important in the distribution

TABLE 4

FREQUENCY DISTRIBUTIONS OF NON-RANDOMLY OCCURRING ACTS DURING DRY-OILING BY ADULTS AND CHICKS[1]

	Action unit												
Adults[2]	1	2	3	4	5	6	7	8	9	10	Total	χ^2	P
Oil	24	20	15	11	12	6	9	5	6	3	111	36.95	0.001
Bill-to-wing-edge	12	6	13	9	8	4	3	1	2	3	61	26.34	0.005
Chicks[3]													
Oil	8	1	0	5	3	2	5	3	0	1	28	21.90	0.01
Bill-to-wing-edge	0	1	2	1	6	0	2	3	4	1	20	16.02	NS
Preen back	4	12	15	19	10	22	13	11	7	7	120	23.16	0.01

[1] The number of times each movement was performed in each action unit is shown. The distribution of all acts listed in Table 1 was random for non-oil sequences by chicks aged 14–20 and 21–28 days and for adults. For chicks aged 7–13 days, only the distribution of breast preening was non-random ($\chi^2 = 33.57$, df = 9, $P < 0.001$), with the highest frequencies occurring in the first 2 action units. An action unit equals 1/10th of a sequence (see Ainley 1974).

[2, 3] The distribution of all other acts listed in Table 1 was random. Bill-to-wing-edge for chicks was included because the distribution approached non-randomness (required χ^2 value for $P < 0.05$ is 16.9).

of oil, significantly fewer times than did adults. (7) As far as the other comfort movements are concerned, chicks and adults rarely showed the same relative frequencies, especially during non-oiling. For example, during non-oiling sequences, chicks showed higher relative frequencies of head-shaking, ruffle-shaking, yawning and rapid-wing-flapping than adults.

Temporal distribution patterns.—For analyzing the distribution of comfort movements within a sequence, each sequence was divided into 10 equal parts, called action units (see Methods). While most comfort movements were found to be distributed randomly throughout a sequence, a few occurred non-randomly (Table 4). Oiling, for example, occurred most frequently in the first 3 action units in dry-oiling sequences of both chicks and adults. Bill-to-wing-edge followed a distribution pattern similar to that of oiling in adults. That both oiling and bill-to-wing-edge followed the same distribution pattern in adults is not surprising, since oiling is frequently followed by bill-to-wing-edge in adult dry-oiling sequences (see below).

In chicks the distribution of bill-to-wing-edge approached non-randomness, but it occurred most frequently during the fifth action unit and thus did not immediately follow oiling. Back preening was the only other comfort movement distributed non-randomly during dry-oiling by chicks. It occurred most frequently in action units 2–8.

The continuity of comfort movements.—Adult penguins tend to treat 1

TABLE 5

THE CONTINUITY OF COMFORT MOVEMENTS BY CHICKS AND ADULTS ACCORDING TO SIDE OF BODY AND AREA DURING 2-ACT TRANSITIONS

	Non-oil sequences				Dry-oil sequences	
	Chicks			Adults	Chicks	Adults
Movements remaining on:	Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6
Same side[1]	65.5% (38/58)	75.3% (204/271)	77.6% (104/134)	70.0% (389/556)	83.7% (461/551)	83.3% (685/822)
Same area[2]	48.3 (28/58)	27.6 (75/272)	21.3 (29/136)	14.1 (79/562)	12.8 (75/586)	8.8 (75/855)
Same side and area[3]	25.9 (15/58)	18.1 (49/271)	12.7 (17/134)	13.5 (75/556)	10.3 (57/551)	7.7 (63/822)

[1] Result of proportions test: 1 = 2, 3, 4; 2 = 3, 4; 3 = 4, 5, 6; 5 = 6 ($Z < 1.96$, $P > 0.05$).
[2] Result of proportions test: 2 = 3; 4 = 5 ($Z < 1.96$, $P > 0.05$).
[3] Result of proportions test: 1 = 2; 2 = 3, 4; 3 = 4, 5, 6; 4 = 5; 5 = 6 ($Z < 1.96$, $P > 0.05$).

side of the body for some time before switching to the other (Ainley 1974). To determine whether this tendency develops gradually during ontogeny, we compared the various groups (Table 5). During non-oil sequences, chicks switched sides more often than adults during transition from 1 act to another. There was a steady increase with age, from 7–28 days, in the tendency of chicks to remain on the same side of the body. By 21–28 days, there was no significant difference between chicks and adults during non-oiling. During dry-oiling, however, chicks remained on the same side of the body less than adults. Nevertheless, in dry-oiling sequences performed by both chicks and adults, there was a strong, significant tendency for acts leading to, and following, oiling to occur on the same side of the body to which the head was turned when gathering oil in the bill from the uropygial gland (greater than 75% for chicks and 85% for adults).

While chicks tended to remain on the same side less often than adults, they remained in the same area (regardless of side) during the transition from 1 act to another, more frequently than adults. Furthermore, in those cases of which the younger chicks (7–20 days of age) remained on the same side of the body, they also tended to stay in the same area of the body. This was also true for both non-oil and dry-oil sequences. Thus, chicks appear to be less effective than adults in distributing the oil to all parts of the body during dry-oiling.

TABLE 6

A COMPILATION OF SELECTED 2-ACT TRANSITIONS FOR DRY-OILING BY CHICKS AND ADULTS FOR WHICH $P < 0.001$ ($Z > 3.29$)

	Chicks		Adults	
2-Act transition[1]	Conditional probability	Z value	Conditional probability	Z value
Oil/BW	–	–	0.40	12.60
Oil/BR[2]	0.24	2.89	–	–
BW/WR[2]	0.81	11.65	0.71	19.32
WR/BR[2]	0.36	5.38	0.14	3.50
SH/side	0.44	14.28	0.32	4.21
BR/belly[2]	0.41	11.80	0.23	5.61
BR/BR	0.22	5.13	–	–
Belly/BR	0.29	5.11	–	–
Side/WR	–	–	0.17	4.80
Side/SR	–	–	0.14	3.18

[1] See Table 1 for code.
[2] Same transitions found during wet-oiling by adults (see Ainley 1974, p. 33).

Two-act transitions

To understand in greater detail the way in which comfort sequences develop and become organized, analyses were performed on transitions between an act and the one immediately following.

Significant transitions.—In all groups, a few instances occurred in which there was a significant transition between a behavior and itself (Tables 6 and 7). That is, the individual performed an action, paused and lifted its head from the body surface, and then immediately performed the same action again. Of the 3 significant transitions within non-oiling sequences in chicks aged 7–13 days, 2 represented a transition between an act and itself. Only this group of chicks differed significantly from all other groups in the proportion of times a transition occurred between an act and itself (proportion test $Z > 1.96$, $P < 0.05$). Data for selected 2-act transitions are presented in Tables 6 (dry-oiling) and 7 (non-oiling), and may be summarized as follows. (1) When chicks aged 7–13 days were included, no 2-act transitions were common to all 6 groups. However, when this youngest group of chicks was excluded, breast/belly and shoulder/side were shared by the remaining 5 groups. (2) Breast/breast, breast/belly and belly/breast were observed in all groups of chicks, during both types of sequences. During non-oiling, 6 of the 8 significant transitions involved the breast area. (3) Bill-to-wing-edge/wing-rub, wing-rub/breast, shoulder/side, breast/belly and cloaca/breast were common to dry-oil sequences by both chicks and

TABLE 7

A COMPILATION OF SELECTED 2-ACT TRANSITIONS FOR NON-OILING BY CHICKS AND ADULTS FOR WHICH $P < 0.001$ ($Z > 3.29$) IN AT LEAST 1 GROUP OF BIRDS[1]

	Chicks					
	14–20 days		21–28 days		Adults	
2-Act transition[2]	CP[3]	Z value	CP	Z value	CP	Z value
BW/WR	–	–	–	–	0.23	3.95
SH/BR	0.24	2.68[a]	0.40	5.00	–	–
SH/side	0.41	5.53	0.27	2.98[a]	0.18	2.25[b]
BR/BR	0.44	14.53	0.30	6.12	0.15	2.32[b]
BR/belly	0.27	7.79	0.23	4.41	0.18	3.31
Back/BR	0.44	5.76	0.30	2.84	–	–
Belly/BR	0.30	5.54	0.40	4.07	–	–
Side/BR	0.32	6.21	0.35	5.24	–	–
Side/WR	–	–	–	–	0.15	3.35
Side/SR	–	–	–	–	0.15	3.35
Leg/leg	0.35	4.91	0.29	3.18[a]	–	–

[1] For chicks aged 7–13 days, there were only 3 significant 2-act transitions: Belly/belly ($P < 0.001$, $Z = 6.62$), BR/BR ($P < 0.001$, $Z = 8.06$), and Belly/BR ($P < 0.05$, $Z = 2.27$).

[2] See Table 1 for code.

[3] CP = conditional probability.

[a] $P < 0.01$.

[b] $P < 0.05$.

adults. (4) When significant 2-act transitions between movements performed on the same side of the body were considered in adult dry-oil sequences, oil/bill-to-wing-edge occurred on the same side of the body 35/37 (95%) times, bill-to-wing-edge/wing-rub occurred on the same side of the body 42/42 times, and wing-rub/shoulder-rub occurred on the same side of the body 10/10 times. (5) During dry-oiling by chicks, the shoulder appeared to be a "pivot" for crossing from 1 side of the body to another. For example, for transitions involving the shoulder (excluding shoulder/shoulder), the chicks remained on the same side of the body only 8/115 (7%) times. In contrast, during dry-oiling by adults and non-oiling by chicks, when transitions involved the shoulder, the birds tended to remain on the same side of the body 10/10 and 41/44 (93%) times, respectively.

DISCUSSION

Age at first appearance of movements.—Adélie Penguins are semi-altricial birds (Nice 1962). Most of the different comfort movements appeared in chicks after 7–9 days of age, in contrast to precocial fowl, ducks and geese, in which many comfort (and other) behaviors are performed within a few days of, or even during, hatching (Nice 1962, McKinney 1965, Dawson and Siegel 1967, Brown et al. 1976). The earliest comfort movements performed were directed to body areas (breast, belly) comprising a major portion of the bird's surface area. In addition, it is these areas of the body that make the most contact with the ground and thus tend to get soiled when the young chick lies down. Later, when the chick begins to stand upright for a greater period of time and beings to walk around, dirt collects on other body areas as well. These changes in posture and activity may then play a role in the change in relative distribution of comfort behaviors during early ontogeny.

The last comfort activities to emerge ontogenetically were shoulder-rubbing (day 33) and oiling (day 35), just after the uropygial gland became functional (days 30–33) and just prior to fledging (going out to sea for the first time: approximately 6–8 weeks of age). That both oiling and shoulder-rubbing appear at approximately the same time is perhaps not surprising since shoulder-rubbing is the specific behavior used to distribute oil from the head to the shoulder, after the oil has been transferred to the head by wing-rubbing (Ainley 1974). A similar relationship was noted by Kruijt (1961) for Burmese Junglefowl (*Gallus gallus spadiceus*) in which head-rubbing, an action used to release oil from the oil gland, appeared simultaneously (day 11) with the development of function of the gland. Wing-rubbing, on the other hand, a behavior that is used in other contexts as well, first appeared in the penguins very much earlier, on day 7.

The appearance of several other comfort movements in Adélie chicks coincided with growth of contour feathers. At approximately 20 days of age, contour feathers began to emerge (Taylor 1962, Spurr 1975, this study). This corresponded to a marked increase in the number of acts per sequence during non-oiling. The oldest chicks still performed fewer acts than adults during non-oiling. The highest rate (8.4 acts/min) and highest number of acts per sequence (63.6) were performed during dry-oiling by adults. Overall, penguin chicks performed more acts per sequence than the terns studied by van Iersel and Bol (1958). Van Iersel and Bol reported that young terns (age not given) performed an average of 1.2 acts in succession, and never more than 6.

A change in the distribution of preening effort also occurred during the fourth week, apparently related to feather growth. For example, down is lost from the legs at about 25 days of age (Taylor 1962): correspondingly, the proportion of leg preening increased from 3.6% in chicks 14–20 days of age to 8.8% in those 21–28 days old. Mergler (pers. comm.) observed a similar trend towards increased preening in areas where down was being lost in Greylag Geese (*Anser anser*).

Dry-oiling compared to wet-oiling.—The mean duration of dry-oiling by adult Adélies (9.4 ± 6.7 min, range 2–24 min) was less than that recorded for wet-oiling. Ainley (1974) reported a range of 2–40 min with an average of approximately 12–15 min for wet-oil sequences. However, the durations of both wet- and dry-oil sequences by the Adélie Penguins were longer than wet-oil sequences recorded either for Mallards (*Anas platyrhynchos*) or White-fronted Geese (*Anser albifrons*) for which the duration of oiling sequences was usually less than 5 min (McKinney 1965). Furthermore, during dry-oiling by young and adult penguins, oiling occurred in a sequence an average of 4.7 and 6.2 times, respectively, compared to 9.0 times per wet-oiling sequence by adults (Ainley 1970). McKinney (1965) reported that Mallard Ducks and White-fronted Geese may oil from 1 to 7 times during an individual oil-preening session, but in the vast majority of sessions the oil gland is used 3–5 times.

The sequence oil/bill-to-wing-edge, the major initial route by which oil is transferred from the oil gland to other body areas, did not occur during dry-oiling by chicks, but did occur during both dry- and wet-oiling by adults (Ainley 1974). In addition, during wet-oiling by adults, wing-rubbing, the action that is used to carry oil to the head, occurred significantly more frequently than during dry-oiling (Ainley 1974:41, Table 6). Wet adults seem more "concerned" with distributing oil around their bodies than are dry adults, and both these groups make more effective attempts to distribute oil than do chicks.

Two-act transitions and the organization of sequences.—In order to gain a more complete understanding of the ontogeny of comfort behavior and the way individual actions become organized into sequences, 2-act transitions were analyzed. There were few highly significant ($P < 0.001$) 2-act transitions common to groups of penguins performing similar types of comfort sequences. The present results combined with those presented by Bekoff (1978) on behavioral variability suggest that although behaviors associated with the gathering and distribution of oil (and some other acts, as well) may be tightly linked in sequence, it is not possible to decipher a "typical" stereotyped comfort movement sequence for each age group. The possibility remains that individuals may show some degree of stereotypy.

Most significant 2-act transitions involved the breast area. For example, of the 5 two-act transitions common to dry-oiling by both adults and chicks, 3 involved the breast. Similarly, of the 8 two-act transitions that were common to non-oil sequences performed by chicks aged 7–13 and 21–28 days, 6 involved the breast area. Van Iersel and Bol (1958) considered breast-preening to be a low-threshold act. Since the breast occupies the largest surface area of any body section in adult Adélies (Ainley 1974) and this also appears to be true in chicks, it it not surprising that it is involved in a large number of 2-act transitions, both those that are common to a number of groups and those that occur only in 1 group.

In addition to extensive preening of the breast by adults and chicks, the shoulder also took on special significance among dry-oiling chicks. During dry-oiling by chicks, the shoulder appeared to be a "pivot" point from which the birds would cross from 1 side of the body to the other. In transitions involving the shoulder (excluding shoulder/shoulder movements), the chicks changed sides 93% of the time. In contrast, in the other groups of penguins, over 90% of the transitions involving the shoulder were on the same side of the body. There is no obvious reason for these differences. During dry-oiling by chicks, shoulder preening did not occur at a specific point in the ongoing sequence, and the posture that the chicks assumed while preening their shoulders during dry-oiling did not appear to differ from the posture that the non-oiling chicks assumed when they preened their shoulders. Possibly a more subtle factor was involved. Perhaps the dry-oiling chicks were trying to make the transition from shoulder preening to gathering oil and in doing so began to lose their balance. The best way to regain balance would be to shift their weight to the other side of the midline. After this shift they might simply continue preening. The fact that the shoulder did not seem to be a pivot point in the younger chicks in which the oil gland was not functional makes this suggestion plausible. In any case, the large difference between the groups seems worthy of further study.

Our data also showed major differences between dry-oiling and non-oiling sequences of comfort movements in adult Adélie Penguins. Furthermore, our developmental data showed a gradual refinement in the organization of non-oil sequences performed by the chicks so that by the time they were 21–28 days of age they resembled adults in a number of ways. Dry-oiling by chicks also shared many common characteristics with dry-oiling by adults. Unfortunately, Adélie Penguin chicks are inacccssible to study soon after they reach 6–8 weeks of age when they fledge and go out to sea, usually for a period of 2–3 years (LeResche 1971). Consequently, behavioral development during this period cannot be studied.

SUMMARY

The development of comfort behaviors in Adélie Penguins and the organization of comfort activities in adults, were studied at Cape Crozier, Ross Island, Antarctica. Non-oiling and dry-oiling (feathers not wet) comfort sequences were compared to one another; these results were then compared to data collected by Ainley (1974) on wet-oiling by adults immediately after they emerged from the sea. For purposes of analyzing the ontogeny of non-oiling comfort activities, chicks were grouped into 3 groups: 7–13, 14–20 and 21–28 days of age. Dry-oiling was observed in chicks 35–43 days of age. Our

results were as follows. (1) Only yawning occurred on the day after hatching. The earliest preening movements appeared on day 7 (breast and belly preening). Oil distribution behaviors appeared between days 30–33, the same period during which the oil gland became functional. The first dry-oiling sequence was observed on day 35. (2) There was no difference in the duration of non-oil comfort sequences between chicks over 13 days of age and adults. Chicks performed fewer acts per min than did adults and therefore the mean number of acts per sequence was lower in chicks. (3) In general, behaviors were randomly distributed throughout comfort sequences. Exceptions include oiling by adults and chicks, bill-to-wing-edge by adults, and back preening by chicks. (4) During transitions from 1 act to another, chicks aged 21–28 days remained on the same side of the body and in the same area with the same relative frequency as non-oiling adults. (5) Dry-oiling by chicks and adults shared many common characteristics: (i) oiling occurred non-randomly in the beginning of the sequences, (ii) the relative frequency of occurrence of breast and belly preening was the same, (iii) during transitions from 1 act to another, the groups did not differ with respect to remaining on the same side of the body and in the same body area, (iv) actions leading to and immediately following oiling occurred very frequently ($> 78\%$) on the same side of the body to which the head was turned when gathering oil in the bill.

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AGONISTIC BEHAVIOR IN SHORT-BILLED DOWITCHERS FEEDING ON A PATCHY RESOURCE

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Aggressive behavior in migratory shorebirds occurs primarily between foraging individuals and probably depends on such factors as density of foraging shorebirds, foraging methods, and density and patchiness of prey items (Recher and Recher 1969, Goss-Custard 1970). Frequency and intensity of aggression varies widely between and within shorebird species (Recher and Recher 1969). In this paper we present evidence that an extremely patchy food resource increases the frequency of agonistic encounters in Short-billed Dowitchers (*Limnodromus griseus*), a species which the Rechers describe as rarely aggressive while foraging.

STUDY AREA AND METHODS

Observations were made on 2 tidal sand flats in Kingston and Duxbury bays, near Plymouth, Massachusetts, between 16:00 and 17:45 on 26 July 1976 (Fig. 1). The description of the behavior is based on observations made through spotting scopes at distances of no more than 150 m. To compare the agonistic foragers with controls, we took the number of bird-sec for the group (number of birds being watched multiplied by the time spent watching) and derived an expected ratio of aggressive encounters assuming an equal rate of encounter in each group. The distribution and abundance of food resources available were measured by taking 69 core samples (10 cm diameter, 20 cm deep) of the substrate at 2 m intervals along parallel transects 2 m apart. Each core was broken free of the substrate, washed on a 1.0 mm mesh screen, and sorted by eye in the field. Our previous experience has shown that this procedure removes 90% of the organisms that are greater than 0.25 cm in length (Schneider 1978). Examination of the stomach contents of 3 birds collected on 24 August 1976 showed that more than 70% of the prey items were greater than or equal to 2 mm in length (94, 81, 73%). The 3 stomachs contained 83, 32, and 15 items, ranging in size from smaller than 1 mm to 5 mm.

RESULTS

Description of the behavior.—Dowitchers in this estuary typically forage in cohesive flocks of non-agonistic individuals that move as groups across the flats. We first noticed agonistic behavior in Short-billed Dowitchers in a flock of 125 birds feeding near the SW edge of H-flat. This flock was confined to an area less than 40 m × 10 m. We observed the same behavior at the same site on the 2 subsequent days, occurring in flocks of about 70–80 and 35 birds respectively. The individuals in the flocks were feeding by probing into the sand with their bills using a combination of the probe-multiple-halting (PrMH) and probe-single-halting (PrSH) foraging

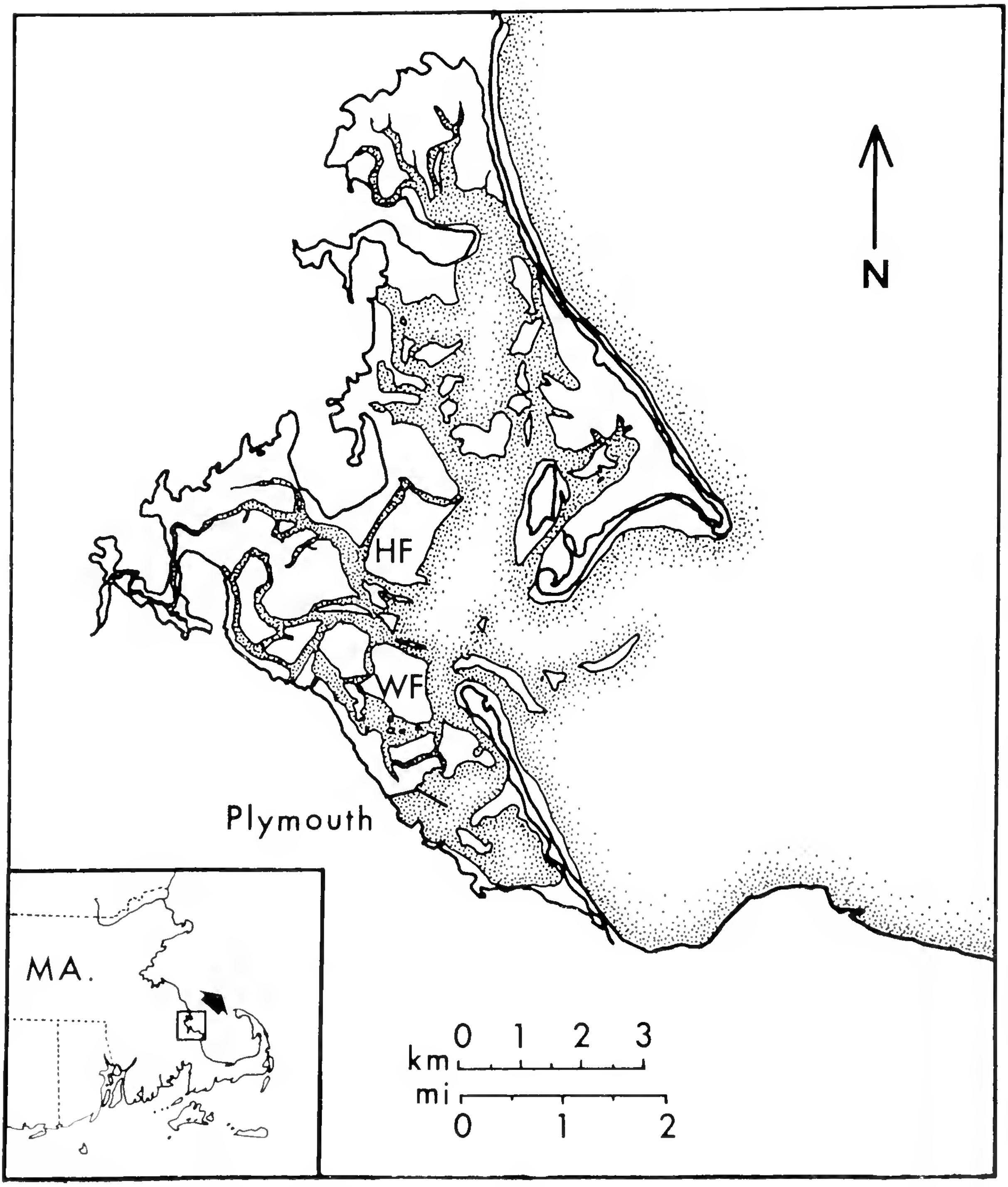

FIG. 1. Locations of H-flat (HF) and White Flat (WF) in Kingston and Duxbury bays where this study was conducted. Inset: location of this estuary on the New England coast.

methods described by Baker and Baker (1973). Individual birds turned frequently, often returning to certain spots to forage rapidly. Aggressive chases were initiated 14 times by successful foragers (seen swallowing after probes) and 15 times by birds intruding on successful foragers. The latter behavior in 10 encounters resulted in a displacement, where an intruder would return to a feeding site after chasing off the successful forager. In 14 other chases the initiator was not determined. In all chases seen, the chaser charged with its body tilted forward so that the tail was above the shoulders but not cocked at the base, wings held against the body, scapular feathers laid flat, neck extended, head low, and bill directed forward and tilted 45° below the horizontal.

Aggressive charges elicited one of 3 responses, all of which prevented direct contact between birds. In 25 of 43 responses to a charge the "chasee" suddenly raised its wings, forming a "V," and jumped up a few decimeters so that only a slight downward stroke of the wings was needed to flutter away a meter or so. In another 17 encounters 1 bird simply ran away, usually less than 1 m. The third response, seen only once, was for a bird to resist displacement by standing its ground. In this circumstance the bird did not remove its bill from the sand but froze as the chaser swerved off from its unsuccessful attack. An agonistic encounter was followed by a repetition of the same behavior, by a reversal when the chasee became the chaser, or by the involvement of a third bird in a second chase.

Other workers in the same bay in 1974 and 1975 observed only 4 instances of aggression involving Short-billed Dowitchers despite approximately 23 h of observation of this species (N. Atkins, pers. comm.; K. Elkins, field notes). None of these instances of aggression resembled the behavior we saw.

Flock dynamics.—We gathered control observations on other flocks of dowitchers during the same tide on H-flat and on another flat in the estuary. One of these flocks, of about 15 birds, was observed foraging immediately following our observations of the agonistic flock on the same sand flat (H-flat), but in an area more normally used by dowitchers. We then observed another flock of about 90 birds foraging on White Flat, a flat similar to H-flat and about 1500 m distant, within 25 min of concluding our observations of the agonistic flock. The area in which these control flocks were feeding had been exposed less than 1 h longer than the area where the agonistic flock foraged. The different flock sizes in our observed groups could be another variable, but in order to make observations close together on the same tidal cycle we had to ignore this possibility.

The number of encounters seen in the agonistic flock and in the control flocks are presented in Table 1. Comparison of the observed rate of encounter with the expected rate showed that there were significantly more encounters (χ^2, $P < 0.005$) in the agonistic flock than in the control flocks (Table 1).

We were impressed by the differences in spacing and movement of individuals in the flock of agonistic birds, relative to control flocks. The

TABLE 1

AGONISTIC ENCOUNTERS WITHIN FLOCKS OF SHORT-BILLED DOWITCHERS[1]

	Mean number of birds watched[2]	Observation period (sec)	Number of encounters[3]	
			Observed	Expected
Flocks foraging on *Limulus* eggs				
H-flat (flock of 70–80)	11.6(9–17)	670	24	14.27
Same flock	6	370	10	4.07
Total			34	18.34
Flocks not foraging on *Limulus* eggs				
H-flat (flock of 15)	15	120	0	3.30
White Flat (flock of 90)	19.8(15–23)	395	2	14.36
Total			2	17.66

[1] Observations were made in Kingston-Duxbury Harbor on 26 July 1976.

[2] The range is given in parentheses if the number of birds changed during the observation period.

[3] Expected values were calculated assuming that the number of encounters is proportional to the number of birds watched and the time spent watching them. The observed rate of encounter among foragers on *Limulus* eggs, compared to controls, far exceeds the expected number ($\chi^2 = 29.21 >> \chi^2_{0.005[1]} = 7.88$).

agonistic birds appeared to be concentrated with smaller distances between birds than normally observed, but we did not quantify this. The agonistic birds remained in the same limited area during our observations, while foraging dowitchers at Plymouth often drift slowly across the flats. Finally, the orientation of individuals in the agonistic flock did not coincide, while individuals in control flocks usually moved in the same direction.

Distribution and abundance of food resources.—Sampling carried out on 25 July to determine what food resources were available to the flock of highly agonistic dowitchers showed that potential invertebrate prey items in the area of the flock differed from the surrounding area. Core samples taken from outside the restricted foraging area of this flock contained little besides a few polychaete worms (*Nephthys caeca* and *Scoloplos robustus*) and a few hundred minute gem clams (*Gemma gemma*). All 3 species are far more common in other areas of this and other sand flats in the bay. The 2 samples taken from within the dowitcher foraging area differed only in that 1 of them contained over 50 eggs of the horseshoe crab (*Limulus polyphemus*). We then sampled at 2 m intervals along parallel transects to examine the distribution of the *Limulus* eggs and found 92 eggs in 8 of 14 samples.

We measured egg distribution within the foraging area again on 26 July by sampling at 2 m intervals along parallel transects through the foraging

TABLE 2

DISTRIBUTION AND ABUNDANCE OF IMPORTANT FOOD ITEMS OF SHORT-BILLED DOWITCHERS FORAGING ON H-FLAT AND WHITE FLAT[1]

	Average density ($\bar{x}$) (per 78.5 cm^2 core)	Degree of aggregation[2]
Clymenella torquata (Maldanid polychaete)	2.482	7.438
Tellina agilis (Tellinid pelecypod)	3.827	11.114
Acanthohaustorius millsi (Haustorid amphipod)	7.632	25.383
Trichophoxus epistomus (Phoxocephalid amphipod)	0.897	3.485
Limulus polyphemus eggs (Merostomata: Arthropoda)	0.261	59.832

[1] The importance was judged from stomach contents of dowitchers collected on White Flat and from the high mortality in these species in areas used by dowitchers. Estimates are based on 272 samples from H-flat and White Flat during July, 1976.

[2] Coefficient of dispersion $= s^2/\bar{x}$; $\bar{x} = \Sigma\ x/n$; $s^2 = (x^2 - (\bar{x})^2(n))/(n-1)$; $N = 272$.

area. The 15 cores contained little other than a large number of *Limulus* eggs in 3 adjacent samples. Thus, the occurrence of *Limulus* eggs was not only restricted to a small area of a sand flat, it was also quite patchy within that area. Table 2 indicates how patchy this resource was compared to other prey items of dowitchers feeding on flats in the Kingston-Duxbury estuary.

Limulus eggs were even more localized than indicated by the measure of spatial aggregation used in Table 2. After mating, the female crab deposits 200–300 eggs in a hole of uniform depth gouged into the substrate in a patch that is no wider than 10–20 cm (Shuster 1950). From our observations and sampling efforts, it was apparent that there were several dozen patches of eggs in the area where the agonistic dowitchers were foraging. Spawning sites are evidently quite aggregated since no *Limulus* eggs were collected from over 200 samples made during July of 1976 in the course of a study by DCS of the food resources available to shorebirds in the Kingston-Duxbury estuary.

The occurrence of *Limulus* eggs is also quite restricted in time. Mating and spawning occur monthly, for a few days during spring tides (Hickman 1967). Thus, the resource would only be available to dowitchers once or twice during their summer stay in the estuary.

TABLE 3

CHANGE IN ABUNDANCE OF HORSESHOE CRAB EGGS IN AN AREA OF INTENSE FORAGING BY SHORT-BILLED DOWITCHERS[1]

Date (1976)	Number of eggs collected	Number of samples (with eggs)	Density of eggs per 78.5 cm² (variance)	Number of dowitchers
25 July	92	14(8)	6.57(3.96)	125
26 July	19	15(3)	1.22(0.88)	75
27 July	no count			35
6 August	16	20(4)	0.8(0.53)	0

[1] Average egg density was estimated by counting the number of eggs found in the 78.5 cm² samples taken at 2 m intervals along 2 parallel transects, each 20 m long, through an area roughly 50 m × 20 m.

Limulus eggs disappeared rapidly from the foraging area on H-flat. Table 3 shows the average density and spatial variation of *Limulus* eggs on 3 succeeding dates, during and after foraging in the area by dowitchers. The average density declined tenfold in 10 days, a significant change (*t*-test, $P < 0.001$). It is possible that the eggs may have been hatching during this period, though no larvae were observed. Our sampling removed 248 eggs, probably a small proportion of the original number. The number of dowitchers feeding at this site decreased as *Limulus* eggs became less abundant (Table 3).

We believe that the flock of unusually agonistic dowitchers was foraging for *Limulus* eggs because (1) these dowitchers confined their activity to a small area where *Limulus* eggs were abundant; (2) other food was far less abundant at this site than in other nearby areas (crustaceans were absent, polychaete worms scarce, and gem clams, the only abundant macroorganism, were an order of magnitude less numerous than elsewhere); (3) the dowitchers were feeding by probing to the full extent of their bills, about 5–6 cm deep, corresponding to the depth of *Limulus* eggs; and (4) dowitchers disappeared from the study site as numbers of *Limulus* eggs declined.

DISCUSSION

We attribute both the change in flock foraging behavior and the increased agonistic behavior of the dowitchers to the patchy distribution of the *Limulus* eggs they were apparently hunting. The restricted dispersion of *Limulus* eggs was probably responsible for the restricted movement of the flock on H-flat. Dowitchers in other areas of the bay foraged in cohesive flocks that moved across the flats. The limited number of food patches generated competition for sites among the birds in the flock because each patch was no larger than an individual dowitcher and there were too few patches to go around. The important difference for the individuals in the flock was an increased variation in foraging success among birds so that some did very well and some very poorly. A bird standing on a patch would have lower search, capture, and handling times compared to birds not standing on a patch. It is possible that perception of differences in success by dowitchers brought about the increased agonistic behavior we observed.

Recher and Recher (1969) reported a group of Sanderlings (*Calidris alba*) feeding in a similar *Limulus* spawning area (there the eggs were visible on the surface and within the Sanderlings' reach). They concluded that some individuals actually had established feeding territories and excluded other Sanderlings at great expense of time and energy for both groups. It was difficult to ascertain if the dowitchers also had established feeding territories because of (1) the continual mixing of individuals and changes in "roles," and (2) the lack of landmarks on the uniform flat.

The distribution of a food resource appears to influence the amount of agonistic behavior occurring among individuals of a foraging flock. Normally, foraging flocks feed in areas where the prey are not in defendable discrete patches and where 1 bird's success is probably equivalent to its neighbor's. In this case, energy expended in agonistic behavior produces little benefit. However, if food items are distributed in discrete, easily defendable patches, as in the case with *Limulus* eggs, then the energetic cost of attempting to acquire or defend a patch may be outweighed by the concentration of a large number of food items and savings in decreased search time.

SUMMARY

In this paper we describe an instance of unusual, agonistic behavior in a flock of migrant Short-billed Dowitchers (*Limnodromus griseus*). We compare this behavior to that of other flocks feeding at the same time at other locations in the same estuary and then present evidence suggesting that this behavior resulted from the patchy distribution of the probable foraging resource of this flock, eggs of the horseshoe crab (*Limulus polyphemus*). We propose that an extremely patchy resource has increased the agonistic behavior within the flock by increasing the variation in foraging success among individuals.

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RELATIONS OF WINTERING CANVASBACKS TO ENVIRONMENTAL POLLUTANTS—CHESAPEAKE BAY, MARYLAND

Donald H. White, Rey C. Stendell and Bernard M. Mulhern

Canvasbacks (*Aythya valisineria*) winter on many bays and estuaries that are polluted with a variety of toxic chemicals; moreover, some birds are exposed to contaminants along migration routes. Canvasback numbers have fluctuated widely from year-to-year, and in some years reproductive success has been poor even with favorable conditions on the breeding grounds. Poor success has been attributed to high mortality rates for immatures and adults, habitat and range reduction, and increased nest predation (Trauger 1974). In addition, environmental contaminants may influence success, since elevated levels of some chemicals in tissues and eggs may have adverse effects on reproduction and survival of birds (Stickel 1973).

Chesapeake Bay is the principal wintering area for Canvasbacks (Bellrose 1976). Since 1972, biologists at the Patuxent Wildlife Research Center have been studying Canvasbacks collected from the Bay to determine levels of organochlorine pesticides, polychlorinated biphenyls (PCB's), and selected heavy metals in tissues, eggs, and food items. In this paper we report the residues of environmental pollutants in tissues of Canvasbacks and their food items from Chesapeake Bay, Maryland, and discuss their relation to possible adverse effects on Canvasback populations. Residues of organochlorines and mercury in Canvasback eggs are reported elsewhere (Stendell et al. 1977).

METHODS AND MATERIALS

The Migratory Bird and Habitat Research Laboratory collected Canvasbacks from Chesapeake Bay, Maryland, during the winters of 1973, 1975 and 1976 for analysis of gastrointestinal (GI) tracts to determine food habits. We obtained the carcasses for chemical analysis from these collections. Samples of Canvasback food items (clams) from Chesapeake Bay also were collected. Birds collected in 1973 were skinned and those collected in 1975 were plucked and the carcasses were analyzed for organochlorines. Prior to analysis, the GI tracts, feet, and beaks were removed. Carcasses were homogenized and a portion of each homogenate was analyzed for organochlorine residues at the Patuxent Wildlife Research Center. Residues in 5% of the samples were confirmed with a gas chromatograph/mass spectrometer. Limits of quantification were 0.1 ppm for organochlorine pesticides and 0.5 ppm for PCB's on a wet-weight basis. Analytical procedures we used for organochlorines are described in detail by Cromartie et al. (1975).

Canvasback tissues analyzed for heavy metals included: livers, 1973; livers, kidneys and wingbones, 1975; and livers and kidneys, 1976. Food samples (clams) also were analyzed for selected heavy metals. All heavy metal analyses were done at the Environmental Trace Substances Research Center, Columbia, Missouri, by atomic absorption spectrophotometry using quantification limits of 0.01 ppm on a wet-weight basis for livers, kidneys and clams, and 0.5 ppm on a dry-weight basis for wingbones.

Data were log-transformed and tested for differences using Student's *t*-test. Residues are reported as arithmetic means ± standard errors; since geometric means were very similar, they were excluded from the tables.

RESULTS AND DISCUSSION

Organochlorines.—Eighty-three % of the 1973 carcasses contained DDE, 62% contained PCB's, and 24% contained dieldrin; 99% of the 1975 carcasses contained DDE and PCB's, and 14% contained dieldrin (Table 1). Differences were detected in carcass residues between the collection periods; only DDE, dieldrin, and PCB's were found in some of the 1973 skinned samples whereas some of the 1975 plucked samples contained a variety of other organochlorines. The 1975 samples contained approximately 60% more DDE and PCB's than the 1973 samples; this difference suggests that a large percentage of the residues may have been present in the skin and attached adipose tissue of the 1975 plucked birds. There were no differences ($P > 0.05$) in carcass residue levels between sexes or ages.

Overall, DDE residues in Canvasback carcasses were low (Table 1), and comparable to the levels measured in control birds in 2 dietary experiments. Haegele and Hudson (1974) fed Mallards (*Anas platyrhynchos*) diets containing 40 ppm DDE for 96 days; 42 days after cessation of treated food, DDE residues in skinned carcasses averaged 33 ppm (wet weight). Eleven months after DDE exposure ceased, carcass residues averaged 9.6 ppm in treated birds and 0.5 ppm in control birds. DDE residues in plucked carcasses of Black Ducks (*Anas rubripes*) fed 10 ppm DDE for 7 months averaged 155 ppm (wet weight); residues in control carcasses averaged about 0.3 ppm (Longcore and Stendell 1977). Two years after exposure ceased, DDE residues in Black Duck carcasses had dropped to 12.2 ppm in males and 3.4 ppm in females. Thus, Canvasbacks from the Chesapeake Bay probably are exposed to low environmental levels of DDE since residues in their carcasses were similar to those found in carcasses of experimental controls.

Dieldrin residues averaged less than 0.2 ppm in Canvasbacks (Table 1). These levels are far below residues in skinned carcasses of Meadowlarks (*Sturnella magna*) (4 ppm) and aquatic birds (9 ppm) found dead in areas treated with dieldrin or aldrin (Stickel et al. 1969, Flickinger and King 1972). Carcasses of Japanese Quail (*Coturnix coturnix japonica*) fed 10 ppm dieldrin for 4.5 months contained an average of 23 ppm (Stickel et al. 1969). Ruddy Duck (*Oxyura jamaicensis*) carcasses from the Delaware

TABLE 1

ORGANOCHLORINE RESIDUES (PPM, WET WEIGHT) IN CANVASBACK CARCASSES FROM CHESAPEAKE BAY, MARYLAND

Chemical	Year[1]	N[2]	$\bar{x} \pm SE$[3]
DDE	1973	24	0.36 ± 0.03
	1975	112	0.56 ± 0.06[a]
DDT	1973		ND[4]
	1975	7	0.18 ± 0.01
DDD	1973		ND
	1975	5	0.11 ± 0.00
Dieldrin	1973	7	0.19 ± 0.03
	1975	16	0.19 ± 0.03
PCB's[5]	1973	18	1.5 ± 0.31
	1975	112	2.7 ± 0.21[a]
Toxaphene	1973		ND
	1975	2	0.17 ± 0.01
cis-chlordane	1973		ND
	1975	9	0.19 ± 0.01
trans-nonachlor	1973		ND
	1975	11	0.14 ± 0.01
Oxychlordane	1973		ND
	1975	5	0.12 ± 0.01
Hexachlorobenzene	1973		ND
	1975	5	0.15 ± 0.03
Heptachlor epoxide	1973		ND
	1975	6	0.11 ± 0.00

[1] Sample size was 29 in 1973 and 113 in 1975.
[2] Number of carcasses having detectable residues.
[3] Arithmetic mean ± standard error; all carcasses having detectable residues were used in calculating means.
[4] Not detected.
[5] Polychlorinated biphenyls quantified on the basis of Arochlor 1260.
[a] Residues between years significantly different ($P < 0.001$, Student's *t*-test, log transformed data).

River (White and Kaiser 1976) contained dieldrin residues (0.24 ppm) similar to Canvasback carcasses.

PCB's in Canvasback carcasses (Table 1) were relatively low when compared to levels in other species: levels in Ruddy Ducks (White and Kaiser 1976) were twice those in Canvasbacks and levels in some Great Cormorants (*Phalacrocorax carbo*) found dead were 150 times greater (Koeman 1973).

TABLE 2

HEAVY METAL RESIDUES IN TISSUES OF CANVASBACKS FROM CHESAPEAKE BAY, MARYLAND

Tissue[1]	Year	Metal	N[2]	$\bar{x} \pm$ SE[3]
Liver	1973	lead	29	0.25 ± 0.02[a]
		cadmium	29	0.59 ± 0.09
		copper	29	59 ± 8
		zinc	29	41 ± 3
		mercury	10	0.24 ± 0.03
		chromium	10	0.02 ± 0.00
	1975	lead	87	0.14 ± 0.01
	1976	lead	70	0.19 ± 0.02
Kidney	1975	cadmium	113	2.3 ± 0.16
	1976	cadmium	69	2.3 ± 0.23
Wingbone	1975	lead	78	7.8 ± 1.0

[1] Residues in liver and kidney are reported as ppm wet weight, and ppm dry weight in wingbone.
[2] Number of samples analyzed.
[3] Arithmetic mean ± standard error.
[a] Lead residues between 1973 and 1975, 1976 significantly different ($P < 0.01$, Student's *t*-test, log transformed data).

Canvasback eggs contained up to 29 ppm PCB's, but the potential effects of these elevated levels on Canvasback reproduction are not known (Stendell et al. 1977). Mallards fed 25 ppm PCB for 2 years showed no reproductive impairment (Heath et al. 1972). Similar levels fed to chickens severely impaired reproductive success (Lillie et al. 1974), and 3 ppm PCB in chicken eggs reduced hatchability (Scott et al. 1975). We found that DDE and PCB residues in Canvasback carcasses were significantly correlated (linear regression analysis, $r = 0.80$, df = 130, $P < 0.01$) as were DDE and PCB's in Canvasback eggs (Stendell et al. 1977).

Toxaphene, chlordane isomers, hexachlorobenzene, and heptachlor epoxide were present in a few 1975 Canvasback carcasses (Table 1). In all cases, residues were less than 0.3 ppm and are below levels suspected of causing problems in avian species. Endrin and mirex were not detected in Chesapeake Bay Canvasbacks.

Heavy metals.—Mercury residues in Canvasback livers (Table 2) were lower than those reported in livers of other field-collected waterfowl (Dustman et al. 1972, Krapu et al. 1973, Fimreite 1974) and only slightly higher than in livers of control birds in dietary experiments (Heinz 1976, Stickel et al. 1977). Cadmium ranged up to 11.6 ppm in Canvasback kidneys (Table 2) and mean residues in livers were identical to those reported for Ruddy Ducks from the Delaware River (White and Kaiser 1976). Kidneys of Mallards fed 2 ppm dietary cadmium contained an average of 2.9 ppm after 60 days (White and Finley 1978); these levels are similar to those found in kidneys of Canvasbacks. Two hundred ppm dietary cadmium produced kidney lesions and inhibited spermatogenesis in adult Mallards but no effects were detected in groups fed 2 or 20 ppm (White et al. 1978).

Overall, lead residues in Canvasback livers were relatively low (Table 2). Birds collected in 1975 had lower lead residues than birds collected in 1973 ($P < 0.02$). Lead levels were similar to those reported in livers of experimental birds (Finley et al. 1976a, Finley et al. 1976b). Dieter (1978) measured a lead-specific enzyme in the plasma of about 400 Canvasbacks; 12% of the sample exhibited less than half of the normal blood-enzyme activity indicating exposure to an elevated amount of lead. In a sample of 9 ducks with abnormal enzyme activity, residues of lead in the livers averaged 0.86 ppm (Dieter 1978). In our study, only 3% of the Canvasback livers contained more than 0.5 ppm lead.

While the residue in liver indicates current exposure to lead, the residue in avian bones indicates the history of exposure to lead from all sources including lead shot. Uptake of lead by bone is rapid and loss is slow. An elevated level (> 20 ppm) in wingbones of an immature bird indicates exposure to a high level of lead, most likely as shot (Longcore et al. 1974, Finley et al. 1976b, R. C. Stendell, unpublished data). Since the period of exposure of adults is longer than that of immatures, an elevated level in the bone of adults may result from exposure to shot during the current or past years or possibly to elevated levels of non-shot lead in the diet over an extended period.

Lead residues in our sample of 78 Canvasback wingbones ranged from 0.6 to 38.2 ppm. No Canvasback gizzards contained lead shot, although 6% of immature and 10% of adult wingbones contained greater than 20 ppm lead. However, there was no difference ($P > 0.05$) between wingbone lead levels of immatures and adults. The frequency of occurrence of shot in gizzards of immature waterfowl was significantly correlated to median wingbone lead levels and percentages of wingbones with greater than 20 ppm lead (White and Stendell 1977).

Chromium residues in Canvasback livers were low, but copper and zinc accumulated to levels higher than any of the other metals (Table 2). These levels were similar to those found in livers of Bald Eagles (*Haliaeetus leucocephalus*) and Ospreys (*Pandion haliaetus*) (S. N. Wiemeyer, unpublished data).

In past years the major food of Canvasbacks wintering on Chesapeake Bay was wild celery (*Vallisneria americana*) (Stewart 1962), but this plant has practically disappeared from the area, probably from increased turbidity

TABLE 3

HEAVY METAL RESIDUES (PPM WET WEIGHT) IN CANVASBACK FOOD ITEMS (WHOLE CLAMS) FROM CHESAPEAKE BAY, MARYLAND

Species	Year	Metal	N(n)[1]	x̄ ± SE[2]
Rangia cuneata	1973	lead	6(150)	0.37 ± 0.07
		cadmium	6(150)	0.06 ± 0.01
		copper	6(150)	3.99 ± 0.24
		zinc	6(150)	6.76 ± 1.00
		mercury	6(150)	all t
		chromium	6(150)	0.32 ± 0.07
Macoma balthica	1975	lead	3(426)	0.56 ± 0.07
		cadmium	3(426)	0.05 ± 0.01
Macoma mitchelli	1975	lead	2(190)	0.28 ± 0.06
		cadmium	2(190)	0.02 ± 0.00
Mya arenaria	1975	lead	3(370)	0.30 ± 0.09
		cadmium	3(370)	0.10 ± 0.04
Mulinia lateralis	1975	lead	1(10)	0.02
		cadmium	1(10)	0.02

[1] N(n) = numbers of pools (number of total individuals).
[2] Arithmetic mean ± standard error.
t = Trace residues less than 0.01 ppm.

and lessened salinity (Perry 1974). As a result Canvasbacks have changed to alternate food sources. Approximately 90% of the Canvasbacks' diet consists of small clams of several species (M. C. Perry and F. M. Uhler, unpublished data). Residues of heavy metals in clams collected in 1973 and 1975 are shown in Table 3. In general, cadmium and lead levels were similar in all species, but copper and zinc accumulated to higher levels in the clam, *Rangia cuneata*, than any of the other metals. Mollusks are known to accumulate high levels of certain metals even when exposed to low concentrations of those metals in the environment (Bryan 1971). Therefore, the relatively low metal residues in Chesapeake Bay clams probably reflect background contamination.

CONCLUSIONS

Canvasback eggs (Stendell et al. 1977) and carcasses from the Chesapeake Bay generally contained low levels of organochlorine pesticides and PCB's. Experimental studies with other waterfowl species suggest that these residues are below levels known to have an adverse effect on avian reproduction and survival. A few samples, however, did contain amounts of DDE or PCB's that approximate the range in which adverse effects may be expected. Similarly, levels of mercury and cadmium are below known-effect levels. Lead residues in most birds were low, although elevated levels in wingbones of some birds indicated a history of past exposure to lead; Dieter (1978) found similar results in Canvasbacks by measuring plasma-enzyme levels in blood. Elevated, sublethal levels of lead may cause some physiological disturbances in birds but the potential effect on survival and reproduction are unknown, as is the significance of relatively high copper and zinc residues in Canvasback livers.

In addition, the effects that cumulative concentrations of toxic chemicals in birds might have on reproduction and survival are poorly understood. Birds with high contaminant burdens might be more susceptible to disease, hunting pressure or nest predation than birds with low levels.

SUMMARY

Studies were conducted to determine the levels of environmental pollutants in Canvasbacks wintering on Chesapeake Bay, Maryland, and their food items, in 1973, 1975, and 1976. Canvasback carcasses were analyzed for organochlorine pesticides and polychlorinated biphenyls; livers, kidneys, wingbones, and food items (clams) were analyzed for selected heavy metals. Overall, levels of toxicants in Canvasbacks were below those levels known to cause problems in other avian species. However, 10% of the samples appeared to have elevated lead levels based on wingbone residues. Copper and zinc residues were high in Canvasback livers but their potential effects are unknown.

ACKNOWLEDGMENTS

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U.S. FISH AND WILDLIFE SERVICE, PATUXENT WILDLIFE RESEARCH CENTER, GULF COAST FIELD STATION, P. O. BOX 2506, VICTORIA, TEXAS 77901; U.S. FISH AND WILDLIFE SERVICE, ENVIRONMENTAL CONTAMINANTS EVALUATION PROGRAM, WASHINGTON, D.C. 20240; AND U.S. FISH AND WILDLIFE SERVICE, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND 20811. ACCEPTED 20 JUNE 1978.

EBBA Research Grants

The Eastern Bird Banding Association is sponsoring two $250 Memorial Grants in aid of research using bird banding techniques or bird banding data. The deadline for receipt of applications is 15 March 1980. Applicants should submit a resume of their ornithological or banding background, the project plan, and a budget to the Chairman, EBBA Memorial Grant Committee: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677.

Colonial Waterbird Group Meeting

The Third Annual Meeting of the Colonial Waterbird Group will be held 25–28 October 1979 at the University of Southwestern Louisiana, Lafayette. Field trips to the Gulf Coast are planned, and a *PROCEEDINGS* will be published as in 1978 and 1979. For information on contributing papers, contact P. A. Buckley, North Atlantic Regional Office, National Park Service, 15 State Street, Boston, Massachusetts 02109. Abstracts must be received by 1 September. For information on registration, write to D. McCrimmon, Laboratory of Ornithology, Cornell University, Ithaca, New York 14853.

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CHANGES IN OLDSQUAW CARCASS WEIGHT

Steven R. Peterson and Robert S. Ellarson

Data on weight changes in the Anseriformes have been reviewed by Falk et al. (1966), Weller (1957), and others. Most of this material relates to summer collections or fall-shot samples (Elder 1946, Bellrose and Hawkins 1947). Ryan (1972) determined live winter weights for several species of diving ducks captured in New York, while Ellarson (1956) examined the winter and spring weights of several thousand Oldsquaws (*Clangula hyemalis*) captured in gill nets on Lake Michigan. Changes in weights of Canada Geese (*Branta canadensis*) wintering in Illinois were noted by Hanson (1962) and Raveling (1968).

Most studies on changes in body weights have not quantified what fraction of these changes was contributed by differences in the fat depot (lipids), water (moisture), or fat-free dry weight (protein, bone tissue, etc.). Our investigation of organochlorine contamination in Oldsquaws (Peterson 1976) dictated we monitor changes in body fat levels because these pesticides are extremely lipophilic. Therefore, the purpose of this study was to: (1) document changes in the weight of Oldsquaws for different sex and age classes through the winter, spring, and summer; and (2) quantify the change in lipid, moisture, and dry weight components through the same time period. These data should lead to a better understanding of the feeding ecology, energy requirements, and survival in this species (Peterson and Ellarson 1977) and place the interpretation of body weight changes in waterfowl on a more firm basis.

METHODS

Oldsquaws wintering on Lake Michigan were obtained from commercial fishermen who found them drowned in gill nets. Birds collected on the breeding grounds were obtained by shooting. Most samples were collected between 1 December and 27 July during the period 1969–71; 2 birds were taken in late October 1970. Birds were weighed to the nearest 5 g, then sexed and aged by several techniques (Ellarson 1956, Peterson 1976).

In this report, we have adopted Hanson's (1963) classification for age categories: (1) juvenile Oldsquaws are less than fully grown and less than 1 year old; (2) subadults are more than 1 year old, and essentially fully grown although the majority of the cohort have not completed their first breeding season; (3) adults are at least 2 years old, fully grown, and the majority of the cohort has completed 1 or more breeding seasons. When adults and subadults are combined in 1 class, they are called matures in this paper.

Terminology.—For the remainder of this paper, the following terminology will be used:

Whole body weight = weight of the specimen when secured.

Carcass weight = whole body weight minus head, wings, feet, feathers, gastrointestinal tract, and reproductive organs.

Moisture = water, expressed as a % of carcass weight or total grams present in carcass as computed from the extracted sample.

Lipids = ether-extractable fat, expressed as a % of carcass weight or total grams present in carcass as computed from the extracted sample.

Dry weight = fat-free dry weight or carcass weight minus moisture and lipids.

Varying degrees of water-soaked plumage presented a major problem in studying body weights of gill-netted Oldsquaws. Birds from fresh catches were often dripping wet, while others that had been lying exposed on fish docks for a week or more were frequently quite dry. Shot specimens were usually dry, but varying amounts of moisture and mud often adhered to the feathers. Consequently, any analyses of these weights included considerable variability just from desiccation and foreign material in the plumage. Even though the weight of water absorbed in the plumage was relatively constant in different sized birds (about 10%, Ellarson 1956), we do not consider either of these wet or dry weights to be representative of the true live body weights. Because these weights would be of dubious value in more critical analyses, we decided to use carcass weights as a basis for comparing weight changes between different sex and age classes as well as time periods. Carcass weights lack 2 sources of variability present in whole bodies: (1) removal of the plumage eliminated the foreign material and absorbed water; and (2) removal of the gullet and gastrointestinal tract eliminated weight differences caused by varying amounts of ingested food.

Component determinations.—Fat, moisture, and dry weight component determinations were made by the Wisconsin Alumni Research Foundation (WARF), Madison, Wisconsin. Carcasses were prepared for analysis by severing the head, clipping the wings off at the distal end of the humerus, removing the feet at the tarso-metatarsal joint, shearing all feathers to within a few mm of the skin, and removing the gastrointestinal and reproductive tracts. All abdominal fat was left in the cavity. The carcass was then weighed to the nearest g, homogenized in a Hobart food chopper, and a 25 g sample removed.

Moisture content was determined by weighing samples before and after drying in a 40°C oven for 72–96 h. Although the 40°C was low, this temperature was necessary to prevent driving off the polychlorinated biphenyls (PCB's) at higher heat ranges. The samples were then ground with 100 g Na_2SO_4 and extracted 8 h on a Soxhlet extractor using 70 ml ethyl ether and 170 ml petroleum ether. An aliquot of the extract was then reduced to dryness, desiccated, weighed, and the amount of ether-soluble lipid determined. At a minimum, the nonpolar ether would extract only the stored fat, but since the samples were desiccated prior to extraction, the structural lipids were presumably removed as well (Sperry 1955, Giese 1967).

Statistical analysis.—The data were grouped by sex and age classes for a particular month then subjected to the Student's *t*-test. Changes that occurred between periods, as well as sex and age classes, were then assessed for significance.

RESULTS

Differences in carcass weights.—Average monthly carcass weights, October through May, were plotted for 5 age and sex classes (Fig. 1). During the

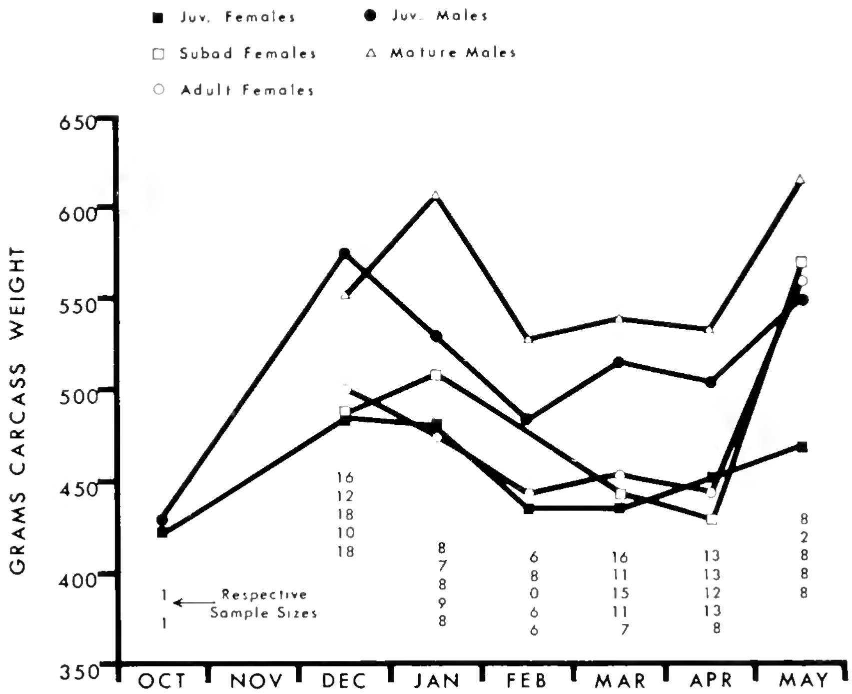

FIG. 1. Average monthly weight of Oldsquaw carcasses collected on Lake Michigan, 1969–71.

winter, carcass weights of Oldsquaws on Lake Michigan were highest during December and January, then declines were recorded through February in mature males, juvenile males and adult females ($P < 0.05$). Subadult females were not sampled in February, but differences were noted in carcass weights between January and March ($P < 0.01$).

Beginning in April, abrupt increases in carcass weights were recorded, especially in Oldsquaws over 1 year old. Between April and May, mature male and female carcasses increased 13 and 24% ($P < 0.01$), respectively. Juveniles also gained weight between April and May, but less than the matures. Juvenile males increased 8% ($P < 0.01$) while juvenile females increased 4% ($P > 0.05$).

In general, carcass weights varied by sex and age. Mature males averaged 15% larger than adult females and differences during the winter and spring were significant ($P < 0.02$) in all months except May. Juvenile males averaged 13% heavier than juvenile females, but differences were significant ($P < 0.01$) only in December, March, April and May. Within the same sex, mature Oldsquaws were generally larger than juveniles, but these differences were smaller than those attributable to a specific sex. Mature males were 6% heavier than juvenile males, and adult females 4% heavier than juvenile females. Mature male carcasses were significantly heavier ($P < 0.05$) than juvenile males only in January and May, and adult female weights did not differ significantly from juvenile female weights except in May ($P < 0.001$).

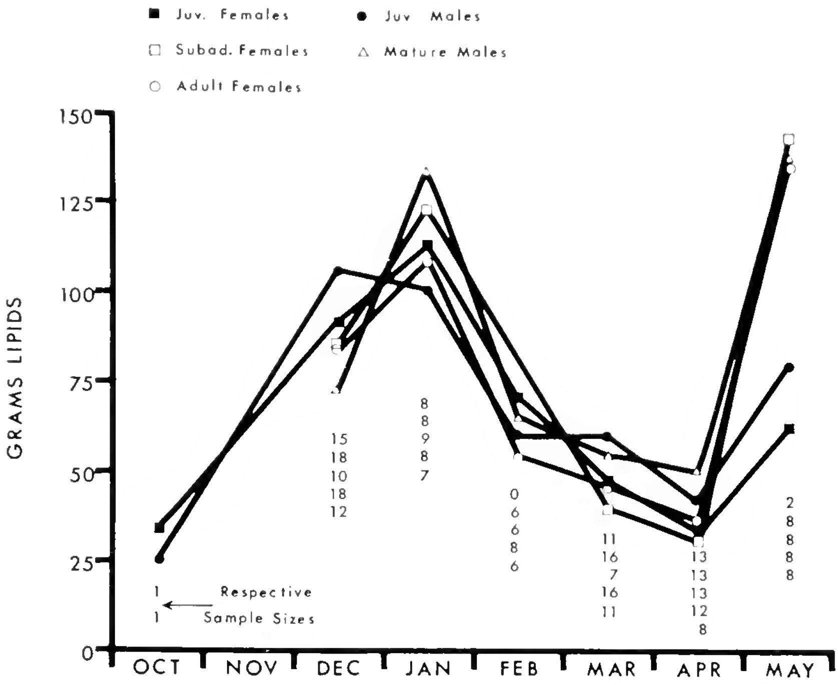

FIG. 2. Average monthly weight of the ether soluble lipid component in Oldsquaw carcasses collected on Lake Michigan, 1969–71.

Differences in lipid weights.—Trends in the ether-soluble lipid fraction (Fig. 2) followed a pattern similar to that observed in carcass weights. Lipid deposition was highest in December or January when an average of 72–106 g of fat was present (19–24% of carcass weight) in the different age and sex classes. Losses of lipids occurred in all sex and age classes from January through April ($P < 0.01$). An average of 58–74% of the lipid fraction was lost during this period so that by April carcasses contained an average of 31–50 g of fat (7–9% of carcass weight), depending on the age and sex class. Between April and May, the lipid fraction of the carcass increased substantially in all age and sex classes ($P < 0.01$). In mature males as well as subadult and adult females, the lipids increased 1.8 to 3.5 times, so that the average weight of lipids in these carcasses was 135–142 g in May (23–25% of carcass weight). Although differences occurred in the weight of the lipid fraction in juveniles between April and May, lipid deposition during this period was not as heavy as in adults because an average of 62–79 g of fat (13–14% of average carcass weight) was present during May versus 135–142 g in matures. The weight of the lipid fraction in all sex and age classes fluctuated together between December and May, but differences among these classes within a month were not apparent except in May when matures were different from juveniles ($P < 0.01$).

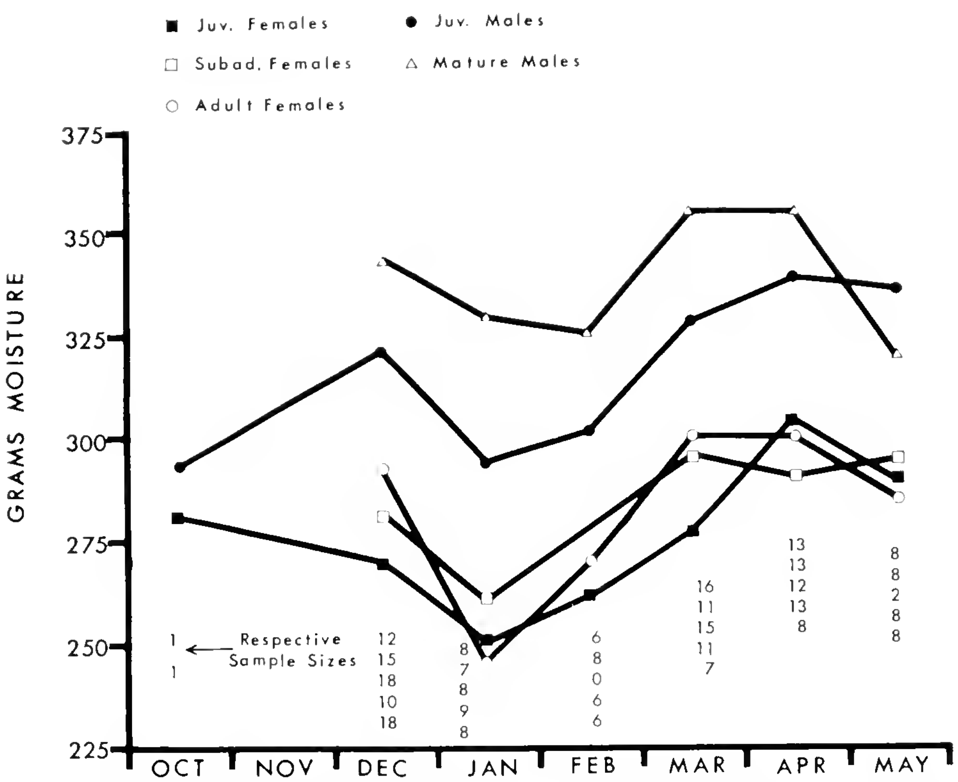

FIG. 3. Average monthly weight of moisture in Oldsquaw carcasses collected on Lake Michigan, 1969–71.

Differences in moisture.—The moisture present in Oldsquaw carcasses during the winter and spring (Fig. 3) generally trended opposite to those shown for lipids and carcass weights. When lipid deposits were high, as in January, moisture content in the carcass was relatively low, averaging 52–56% depending on the age and sex class. In April, when the lipid content and carcass weights were relatively low, the moisture fraction was high, averaging 66–68%. Between December and January. declines in moisture content were noted in all age and sex classes, but the only significant difference occurred in adult females ($P < 0.01$), where moisture dropped 16%. There was a generally increasing trend in moisture content between January and April ($P < 0.001$) for juvenile males, juvenile females, and adult females, followed by a decrease in moisture between April and May (significant only in mature males, $P < 0.05$).

Relative differences in moisture content between age and sex classes for a given month were similar to those exhibited in carcass weights. Mature male carcasses were heavier and contained more moisture than adult females for all months during the winter and spring except May ($P < 0.01$). However, the % moisture in the carcasses during the same month was essentially the same for mature males and adult females as well as for juvenile males and females.

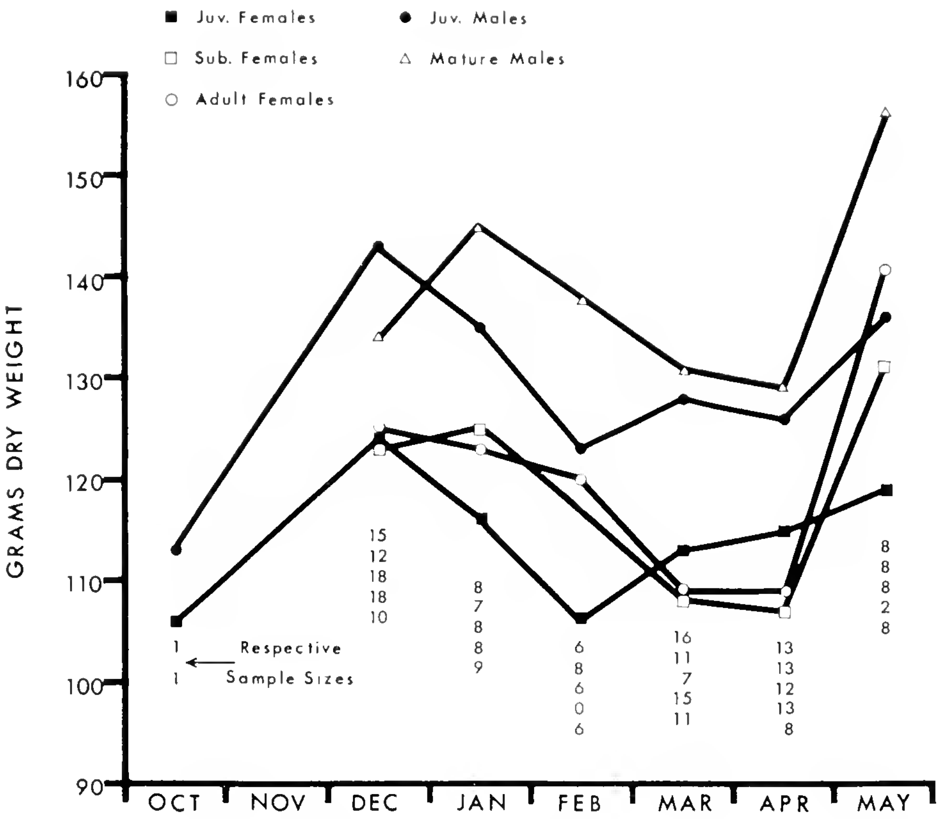

FIG. 4. Average monthly fat-free dry weight of Oldsquaw carcasses collected on Lake Michigan, 1969–71.

Differences in fat-free dry weight.—A peak in dry weight was reached between December and January, followed by a general decline through the remainder of the winter with increases occurring again between April and May (Fig. 4). Differences in dry weight of the carcasses between January and April occurred in mature males, adult females, and subadult females ($P < 0.02$), while differences between April and May were only recorded between males and adult females ($P < 0.01$).

Differences in dry weight between age and sex classes for a specific month were also examined. The dry weights of mature male carcasses were different from those of adult females for all months January through April ($P < 0.02$), but not in December and May. Juvenile male and female dry weights were different during December, February, March and May ($P < 0.05$). Dry weights of mature males were different from those of juvenile males in February and May, while dry weights of adult females were different from those of juvenile females only in May ($P < 0.05$).

Changes in adult female carcass components on the breeding grounds.—Table 1 summarizes changes in carcass components of adult females from just prior to spring migration on Lake Michigan until broods appeared on a breeding ground in northwest Hudson Bay. Carcass weights declined steadily through this period. Approximately 13% of the carcass weight was lost between each of the 4 major periods sampled. Overall, adult females lost an average of 35% of their carcass weight between the middle of May and the end of July.

While carcass weights were declining, no changes were noted in moisture content. There was a difference of only 8% between the average weight of moisture in birds on Lake Michigan prior to migration and birds analyzed just after the broods hatched.

There was a considerable loss in average dry weight of the carcasses over the period. Dry weights declined from an average of 141 g on Lake Michigan to 98 g in females accompanying broods in the Arctic (–31%, $P < 0.02$).

The greatest loss in weight occurred in the lipid fraction. On Lake Michigan prior to migration, adult females had deposited an average of 135 g of lipids, or 24% of their carcass weight was fat. Paired females collected on the breeding grounds 25 days later averaged 81 g of fat (17% of carcass weight). Forty percent of the lipid fraction may thus have been lost on spring migration, if we assume that the pre-migratory lipid reserve of birds collected in the Arctic were similar to those of the Lake Michigan birds.

These data give some insight on the amount of stored energy available to migrating Oldsquaws. A weight loss of 54 g of fat (135–81) represents about 513 kcal metabolized. If the bird is migrating (estimated migration rate at 3.22 kcal/h × 8 for flight) it would metabolize 25.76 kcal/h. The existence energy for a 900 g bird is about 158 kcal/day (6.58/h). If an Oldsquaw migrates 7 h and "exists" 17 h a day, it would require about 292 kcal/day during migration. This suggests Oldsquaws could do this for 1–2 days on that quantity of fat lost, but the birds most likely feed during the day, thereby increase flight time and range.

During the egg-laying period, a 69% loss in the fat reserve reduced the lipid fraction, on the average, from 81 g to 25 g. Therefore, when the females started incubating, 6% of their carcass weight was fat. By the time the eggs hatched, 72% of this remaining lipid fraction had been lost, so that by 1 August, carcasses of adult females contained less than 2% fat. Over the whole period, then, from just prior to migration until just after the eggs hatched, adult females lost 95% of their fat reserve.

These data indicate that most of the change in adult female carcass weights during the breeding season is due to changes in the lipid reserves. Table 1 indicates that 66% of the weight loss in adult female carcasses was accounted for by the 95% loss in body fat reserves. Changes in the dry weight accounted for another 31%, and moisture accounted for only 8%.

TABLE 1

CHANGES IN ADULT FEMALE OLDSQUAW BODY COMPONENTS PRIOR TO SPRING MIGRATION AND ON THE BREEDING GROUNDS[1]

	Approximate date	Sample size	Ave. ± SE carcass weight (g)	Ave. ± SE weight of moisture (g)	Ave. ± SE fat-free dry weight (g)	Ave. ± SE weight of lipids (g)
Lake Michigan, prior to migration[2]	15 May	8	561 ± 14 *	285 ± 11	141 ± 8	135 ± 19 *
Paired females on breeding grounds[2]	10 June	10	486 ± 11 *	277 ± 5	128 ± 2	81 ± 7 *
Incubating females[2]	10 July[3]	11	427 ± 9 *	281 ± 6	121 ± 5	25 ± 3 *
Females with broods[2]	27 July	3	367 ± 20	262 ± 14	98 ± 2	7 ± 2
Total weight loss			194	23	43	128
Percent overall weight loss			35	8	30	95

[1] Samples from Lake Michigan and the Arctic may not be from the same population.
[2] Stage of breeding cycle.
[3] Examination of egg contents indicated clutches had been incubated ca. 3 days.
* Indicates 2 periods different at the 0.02 level of significance.

This is essentially the same relationship observed in different age and sex classes of Oldsquaws on the wintering grounds. The moisture tends to compensate for some losses in the dry or lipid weights, but not enough to keep carcass weights constant. Any substantial change in carcass weight is caused by changes in both the dry weights and the lipid reserves, but primarily the latter.

Composite samples of Oldsquaw eggs averaged 13.7% lipids. The average whole fresh weight of an Oldsquaw egg is 42.7 g ($N = 77$), of which 5.9 g is fat. If the average Oldsquaw clutch is 6.8 eggs (Alison 1975:17), then an adult female transfers an average of 40.1 g of lipids per clutch. Adult females lose an average of 56 g of lipids between the time they arrive on the breeding grounds and the time they commence incubation (Table 1).

Gross internal examination of adult female Oldsquaws collected on the breeding grounds suggested reduced food intake. Food was seldom found in the gullet or gizzard, and the liver, as well as the entire digestive tract, was much reduced when compared with birds collected on Lake Michigan in

May. The data in Table 1 indicate these birds would have had to feed regularly during this period. If one calculates kcal available from the 128 g of fat and 43 g of fat-free dry weight lost between the time the birds left Lake Michigan and the end of incubation, you get approximately 1400 kcal at maximum conversion efficiency, or a total of 8–9 days survival. Of those 1400 kcal, 381 (40.1 lipid × 9.5 kcal/g lipid) go into eggs. Therefore, 1019 kcal/158 kcal/day existence leaves only 6 days of survival without food. If one includes the calories necessary to convert adipose fat to egg lipid, the fat necessary for egg production then, must account for a substantial portion of the lipids lost during the egg-laying period.

DISCUSSION

Relationship of body weight to sex and age.—Age-related weight variations in Oldsquaws are not as apparent as differences associated with sex, but adults averaged heavier than juveniles. Hanson (1962) also showed this to be true in Canada Geese, and Bellrose and Hawkins (1947) found a similar relationship in several species of ducks. Differences in the weight of Oldsquaws related to age were about ⅓ as much as those associated with sex. Bellrose and Hawkins (1947) found this difference in several other species of ducks to be about ½ the difference associated with sex. On a monthly basis, our Oldsquaw data indicate these differences can vary from −4% to +15%. Therefore, age-weight measurements collected over a short time period could be misinterpreted as to whether real differences exist throughout the year between juveniles and adults.

Connell et al. (1960) showed that the fat-free weight of males averaged significantly greater than females, and adults averaged larger than juveniles, but not when individuals of the same wing length were compared. In other words, individuals of the same wing length do not differ in weight because of sex or age (Rogers and Odum 1964). Data we collected on the Oldsquaw indicated a strong relationship between wing length and carcass weight ($r = 0.5$, $P < 0.001$), but wing length was actually a poor physical measurement to separate sex and age differences in carcass weight. Up to ⅓ of an Oldsquaw carcass can be fat, depending on the condition of the bird, and since wing length is relatively constant in an adult bird, considerable variation is encountered as fat is deposited or metabolized. Consequently, only 25% of the variability in carcass weight was accounted for by wing length.

Relationship of body weight to time.—Several hypotheses have been suggested to explain decreases in weight through the winter, the most common being a negative energy balance related to temperature or lack of food. However, Kirkpatrick (1944) found the weights of pen-reared Ring-necked

Pheasants (*Phasianus colchicus*) fluctuated similarly to weights of wild-caught birds, and in Canada Geese weight losses have occurred under *ad libitum* food and water conditions (Raveling 1968).

Oldsquaws are known for their ability to dive to extreme depths (in excess of 45 m; Schorger 1951, Ellarson 1956) to secure their bottom-dwelling foods (primarily deep water amphipods [*Pontoporeia affinis*]; Ellarson 1956, Peterson and Ellarson 1977). When Lake Michigan is free of ice, Oldsquaws are commonly seen diving in 23–38 m of water. During January and February, skim ice can extend for several km offshore, and this forces the birds to feed in deeper water. The decrease in lipid reserves from January to April is probably caused by the birds being forced to make deep dives in which the energy expended to obtain food exceeds that derived from the material ingested. If Oldsquaws are concentrated by ice in water so deep that food cannot be secured, they would die in a matter of weeks. Only on rare occasions does the lake become so completely ice covered that Oldsquaws die of starvation (Gromme 1936, Kumlien and Hollister 1951).

Relationship between carcass components.—Our data on the Oldsquaw indicate lipid weight and dry weight vary together. These data are consistent with other studies that show the degradation of protein and lipids are interlinked. Benedict and Lee (1937:4) concluded a fasting goose first draws upon its glycogen reserves but then "drafts are made almost exclusively upon body fat, although there is a fairly constant draft upon protein representing usually about 10% of the total catabolism." Similar relationships between fat and nonfat weights have been demonstrated in the Bullfinch (*Pyrrhula pyrrhula nesa*; Newton 1969) and Slate-colored Junco (*Junco hyemalis*; Helms et al. 1967). Fry et al. (1970) also noted an increase in the fat-free dry weights during the first few days of fattening prior to migration.

The relationship of moisture to dry and lipid weights is not as clear in the literature as the interrelationship between the latter 2 components. Odum et al. (1964) maintain that during migration "fat is added to and used from pre-existing tissue spaces without appreciable change in the water content or the nonfat dry weight of the body as a whole." On the other hand. Fry et al. (1970) found that the moisture content increased along with the fat-free dry weight when the birds were fattening, while McGreal and Farner (1956) found the water content decreased as the pre-migratory deposition of fat developed. Our data essentially agree with Helms et al. (1967) who found moisture varied inversely with lipids, and also support their conclusion that early fat deposition replaces water concurrent with an addition of dry weight.

Importance of increased dry weight and fat deposition.—Child (1969).

Evans (1969), and other authors generally attribute the spring increase in dry weight as an adaptation to increased flight power for migration, but this does not explain the December–January increase observed on the wintering grounds. The Oldsquaw, as in all alcids and penguins, extends its wings while diving (Johnsgard 1965). On the breeding grounds, most of the diving is limited to shallow tundra ponds, but on Lake Michigan, diving is performed in much deeper water. The winter increase in dry weight could be an adaptation to deep diving. That is, breast muscles, besides being used to help propel the bird through the water with its wings, may be used as a large myoglobin storage area for oxygen.

Fat deposition serves 2 important functions in the Oldsquaw: as fuel during migration, and as energy reserve for a few days during periods of stress on the wintering grounds. The invertebrate bottom fauna on Lake Michigan is the principal food source of Oldsquaws wintering on the lake and consequently is a critical factor in the survival of this population. Any influences adversely affecting the bottom fauna will also adversely affect Oldsquaws.

SUMMARY

Oldsquaws were collected from commercial fishing gear between December and May on Lake Michigan, and in the Arctic during the breeding season. Carcasses were analyzed for lipids, moisture, and dry weight content.

Males were heavier than females in the same age class, and matures were heavier than juveniles in the same sex class, but differences were not always significant within a particular month.

Carcass weights varied seasonally with the heaviest weights being recorded in January and May and the lightest birds being found in April and late summer.

During the summer, adult females steadily lost weight from the time they arrived on the breeding grounds in early June until the eggs hatched in early August. During the winter and spring, changes in the carcass weight as well as the component fractions varied together in the different age and sex classes.

Trends in the lipid and dry weight fractions were similar to those exhibited in carcass weights, but the moisture fraction generally varied opposite to lipids and dry weight.

Most of the seasonal variability in carcass weight could be accounted for by changes in the lipid fraction.

ACKNOWLEDGMENTS

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DEPT. OF WILDLIFE ECOLOGY, UNIV. OF WISCONSIN, MADISON 53706. (PRESENT ADDRESS: SRP: DEPT. OF WILDLIFE RESOURCES, UNIV. OF IDAHO, MOSCOW, IDAHO 83843.) ACCEPTED 25 NOV. 1977.

REQUEST FOR ASSISTANCE

Least Tern sightings.—I have initiated research on the population dynamics and site requirements of Least Terns on the Texas coast to identify possible causes of a recent decline in breeding pairs. Both adult and young terns will be marked with colored patagial tags (streamers) during the 1979, 1980, and 1981 breeding seasons. Tags will be placed on both wings and will bear a single letter and digit for individual recognition of birds. Anyone observing Least Terns marked in this manner is requested to record the following: *date, time, specific location, tag color, alphanumeric symbol, general activity, plumage, association with other birds, observation distance and direction,* and *name, address, and telephone number of observer.* Also, further information is needed concerning concentration areas (feeding, loafing, courting, nesting) used by Least Terns in Texas. Information recorded on such sites should include that requested above, excluding tag description. Please send all information to: Bruce C. Thompson, Dept. of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843. Also, report sightings of marked terns to: Bird Banding Laboratory, Office of Migratory Bird Management, USFWS, Laurel, Maryland 20811.

Zoological Nomenclature Announcement

The required six months' notice is given of the possible use of plenary powers by the International Commission on Zoological Nomenclature in connection with the following name listed by case number (see *Bull. Zool. Nom.* 35, part 3, 19 February 1979):

2233 *Sterna cerulea* Bennett, 1840 (Aves): proposed conservation under the plenary powers.

Comments received early enough will be published in the *Bulletin of Zoological Nomenclature.* Responses should be sent in duplicate (if possible within 6 months of the date of publication of this notice in *Bull. Zool. Nom.* 35, part 3) to R. V. Melville, The Secretary, International Commission on Zoological Nomenclature, c/o British Museum (Natural History), Cromwell Road, London, SW7 5BD, England.

Wilson Bull., 91(2), 1979, pp. 301–316

EFFECTS OF PINE-OAK CLEARCUTTING ON WINTER AND BREEDING BIRDS IN SOUTHWESTERN VIRGINIA

Richard N. Conner, Jerry W. Via and Irvine D. Prather

Clearcutting is a quick and economical method of obtaining needed timber. Many groups, however, oppose clearcutting because of aesthetic reasons, erosion, and effects on wildlife. At present, there is little information available to determine the impact of clearcutting on many wildlife species.

Most studies of succession and bird populations in hardwood forests have reported a general increase in bird species richness and density with increasing age of the sere: Michigan (Kendeigh 1944), North Carolina (Odum 1950), Georgia (Johnston and Odum 1956), Illinois (Karr 1968), and Arkansas (Shugart and James 1973). In contrast, Bond (1957) observed the highest number of species at intermediate stages of succession in Wisconsin.

The gradual trend toward an increase in bird species diversity in southeastern deciduous forests reported by Johnston and Odum (1956) and Shugart and James (1973) was not observed by Conner and Adkisson (1975) in seral stages of regenerating clearcuts in southwestern Virginia. Conner and Adkisson (1975) observed highest breeding bird diversity and numbers in clearcuts 3 to 12 years old. Similar results were also found by Ambrose (1975) in 3-year-old Tennessee clearcuts and in clearcuts up to 6 years old in Southwestern Virginia (Hooper 1967). This is in contrast to what would have been predicted by correlations between foliage height diversity and bird species diversity (MacArthur and MacArthur 1961). The 3- to 12-year-old clearcuts in the study by Conner and Adkisson (1975) included areas of sparse and dense vegetation because of extensive stump sprouting. Where such patchy conditions occur, bird species diversity is no longer solely dependent on foliage height diversity (MacArthur 1964).

Few studies exist on the effect of even-aged management on bird populations in coniferous forests. Studies of succession in coniferous forests and bird populations indicate that bird species diversity increases with age of the sere. Johnston and Odum (1956) reported an increase in number of species, density of breeding pairs, and diversity as the age of the pine (*Pinus* spp.) forest stage of old field succession increased. Peak bird density occurred in mature pine forests where the understory was not inhibited. Haapanen (1965) also reported that breeding bird density and species richness reached a maximum in climax pine stands in Finland. However, species richness was highest in the middle stages of succession of Douglas-fir

(*Pseudotsuga menziesii*) in Oregon (Meslow and Wight 1975). Hole-nesters increased in numbers as the age of the Douglas-fir seres increased.

Our study was designed to see if numbers and diversity of birds in regenerating pitch pine (*Pinus rigida*)-oak (*Quercus* spp.) clearcuts followed successional patterns similar to other coniferous communities (Johnston and Odum 1956, Haapanen 1965) or whether they were different as in regeneration of oak-hickory (*Carya* spp.) clearcuts (Conner and Adkisson 1975). We were also interested in determining the net effect of pine-oak clearcutting on bird populations.

THE STUDY AREAS

Four habitat ages were selected for the study: 3-year-old clearcuts (mean basal area [BA]: 0.8 m^2/ha, vegetation height [VH]: 1.5 m, mean density of stems [DS]: 91.7 stems > 7 cm DBH [diameter at breast height]/ha); 10-year-old clearcuts (BA: 9.2 m^2/ha, VH: 3.5 m, DS: 5395.8 stems > 7 cm DBH/ha); 30-year-old stands (BA: 23.3 m^2/ha, VH: 7.0 m, DS: 3025.0 stems > 7 cm DBH/ha); and mature 80-year-old stands (BA: 36.1 m^2/ha, VH: 20.0 m, DS: 1075.3 stems > 7 cm DBH/ha) (N = 16 for vegetation measurements in each age class). The rectangular study areas, ranging between 20 and 30 ha, were located in the Jefferson and George Washington National Forests. The study areas were typical of the habitat conditions created by clearcutting in the pine-oak timber type of southwestern Virginia. For white pines (*Pinus strobus*), the site index (height in feet that white pines will grow in 50 yrs) in the study areas was around 70. The study areas faced southwest to southeast and were at elevations between 580 and 620 m above sea level. All areas were pitch pine-oak forest type. The most dominant tree species in order of abundance were pitch pine, chestnut oak (*Quercus prinus*), table-mountain pine (*Pinus pungens*), northern red oak (*Quercus rubra*), white pine, white oak (*Q. alba*), and red maple (*Acer rubrum*). Sassafras (*Sassafras albidum*), mountain-laurel (*Kalmia latifolia*), and *Vaccinium* spp. were interspersed throughout the areas.

No site preparation had been done on the clearcut areas prior to planting of pine seedlings. There were no records of, nor could we find any evidence of herbicide application on any of the study areas. Although several pines of 10 cm DBH or more were left standing in each cut area, there were no obvious cavities in snags or live trees for cavity nesting birds. Degrees of cover in the understory can best be seen in photos of each area: 3-year-old (Fig. 1), 10-year-old (Fig. 2), 30-year-old (Fig. 3), 80-year-old (Fig. 4).

METHODS

Four 100 m transects were located in each of the 4 seral stages. Bird species and numbers were censused by counting all birds seen or heard within 25 m of either side of the transect. Care was taken not to census any bird twice; a minimum of 20 min was spent sampling each transect. Transect sample methods have been used in other studies which involved censusing breeding birds in coniferous stands of different ages (Haapanen 1965). If factors other than bird population differences have minimal effect on within and among variation, transect sampling provides excellent data to obtain relative differences between levels of treatment. Absolute measures of bird populations are not needed, and are actually unattainable. The transect method is also an efficient means

Fig. 1. The 3-year-old study area.

of sampling avian populations during breeding and non-breeding seasons (Emlen 1971). Although not as thorough, bird population estimates from transect counts compare favorably with the more tedious spot map method (Graber and Graber 1963, Franzreb 1976). The spot map method is applicable only during the breeding season (Franzreb 1976).

The 16 transects were each sampled 6 times each season. This yielded 24 samples of each seral stage for the winter, and breeding season. Winter birds were censused

FIG. 2. The 10-year-old study area.

between 08:00 and 12:00 EST from January to March 1976. Breeding birds were censused between 06:00 and 10:00 EST during May and June 1976. Sampling times for each area were rotated so that all transects were sampled at all times available in the censusing time period.

We felt 6 replications of each census provided an accurate estimate of the birds in the transects. Several studies have shown that with 4 replications 96% of the bird species in an area were sampled at least once (Palmgren 1930, Dobrakhotov 1961). Our extended sampling period for each season allows for maximum opportunity to sample for all possible winter residents or breeding birds (Kendeigh 1944, Emlen 1971).

Relative abundance and an index of bird species diversity were calculated using the Shannon information formula (Shannon 1948). These values were calculated for each seral stage during both seasons of the study. The Shannon formula is an index for species diversity (H') which has 2 major components: the number of species or species richness (S) and the evenness of species distributions or equitability (J') (Tramer 1969). Species richness typically increases as the structural diversity of the habitat increases (MacArthur and MacArthur 1961). Equitability (J') of bird populations is affected by factors causing changes in spatial arrangements of birds. Typically, equitability is higher during breeding seasons when birds are more evenly spaced due to territoriality and lower during winter when many feeding flocks are formed (Tramer 1969, Kricher 1972).

FIG. 3. The 30-year-old study area.

Tests of the data detected minor deviations from normality. Results of non-parametric 1-way ANOVA (Kruskal-Wallis) and parametric ANOVA revealed the parametric technique to be the more rigorous test. When statistical assumptions can be approximately met, use of parametric techniques rather than non-parametric ones is recommended (Sokal and Rohlf 1969).

FIG. 4. The 80-year-old study area.

RESULTS

Winter

During the winter, bird species diversity and number of birds seen in the 3-year-old pine-oak clearcuts were significantly lower than in the other 3 habitat conditions ($P \leq 0.01$, Duncan's New Multiple Range Test). Bird

TABLE 1

RELATIVE ABUNDANCE OF BIRD SPECIES IN THE 4 STUDY AREAS DURING THE WINTER SEASON

Bird species	3-year-old clearcuts	10-year-old clearcuts	30-year-old stands	Mature stands
Dark-eyed Junco (*Junco hyemalis*)	0.143	0.011		0.005
Black-capped Chickadee (*Parus atricapillus*)	0.286		0.022	0.207
Carolina Chickadee (*Parus carolinensis*)	0.571	0.347	0.389	0.174
Yellow-rumped Warbler (*Dendroica coronata*)		0.011		
Golden-crowned Kinglet (*Regulus satrapa*)		0.274	0.156	0.131
Red-breasted Nuthatch (*Sitta canadensis*)		0.168	0.144	0.131
Tufted Titmouse (*Parus bicolor*)		0.032	0.078	0.047
Blue Jay (*Cyanocitta cristata*)		0.032	0.044	0.005
Fox Sparrow (*Passerella iliaca*)		0.042		0.014
Red Crossbill (*Loxia curvirostra*)		0.021	0.089	0.080
Common Crow (*Corvus brachyrhynchos*)		0.011		0.005
Downy Woodpecker (*Picoides pubescens*)		0.021	0.022	0.023
Cardinal (*Cardinalis cardinalis*)		0.011		0.009
White-breasted Nuthatch (*Sitta carolinensis*)		0.011	0.011	0.066
Pileated Woodpecker (*Dryocopus pileatus*)		0.011		0.009
Common Grackle (*Quiscalus quiscala*)			0.033	
Hermit Thrush (*Catharus guttata*)			0.011	
Carolina Wren (*Troglodytes ludovicianus*)				0.019
Ruby-crowned Kinglet (*Regulus calendula*)				0.005
Brown Creeper (*Certhia familiaris*)				0.019

TABLE 1 (continued)

Bird species	3-year-old clearcuts	10-year-old clearcuts	30-year-old stands	Mature stands
Pine Warbler (*Dendroica pinus*)				0.047
Winter Wren (*Troglodytes troglodytes*)				0.005
Number of birds	14	95	90	213
Species diversity (H′)	0.96	1.82	1.87	2.34
Number of species (S)	3	14	11	19
Equitability (J′)	0.874	0.690	0.780	0.795

species diversity and numbers of birds seen in the mature pine areas during the winter were significantly higher than in the other 3 habitat conditions ($P \leqslant 0.01$). There were no significant differences between the 10- and 30-year-old clearcuts. Equitability index values (J′) of bird species distribu-

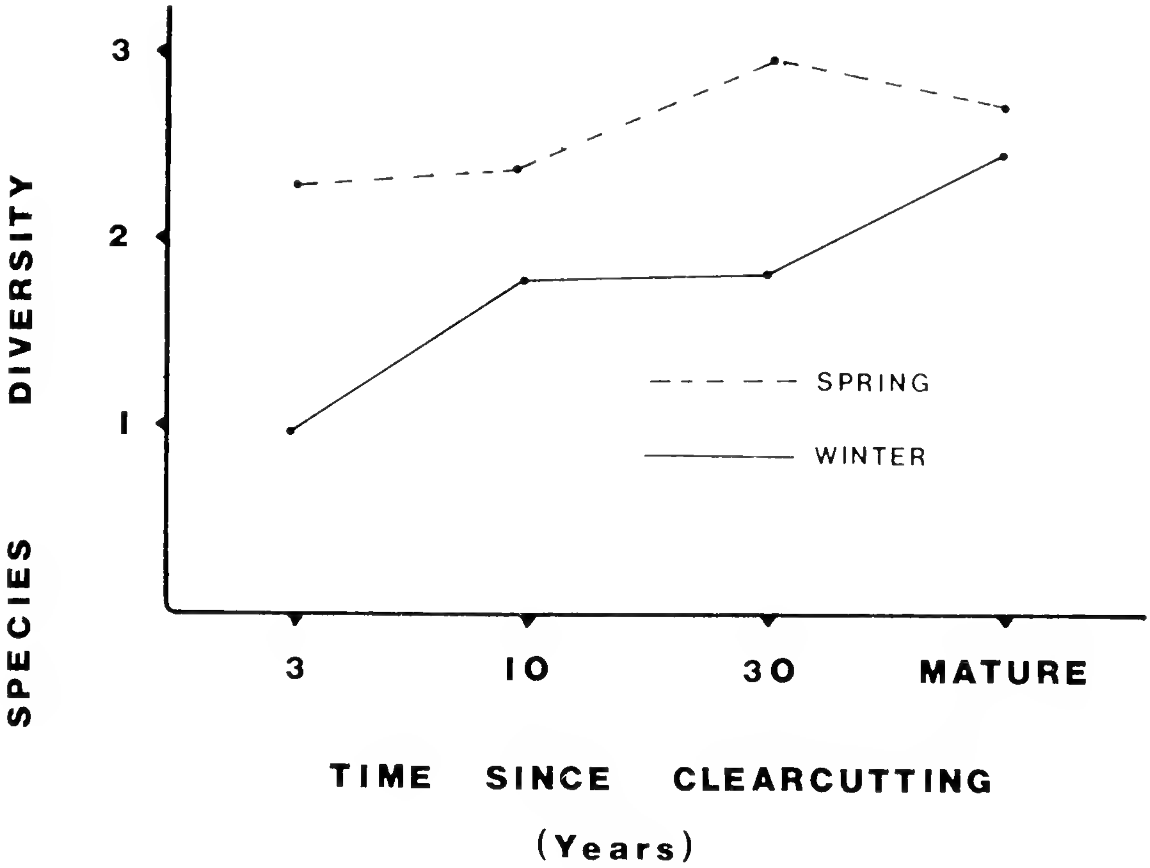

FIG. 5. Bird species diversity in the winter and breeding seasons.

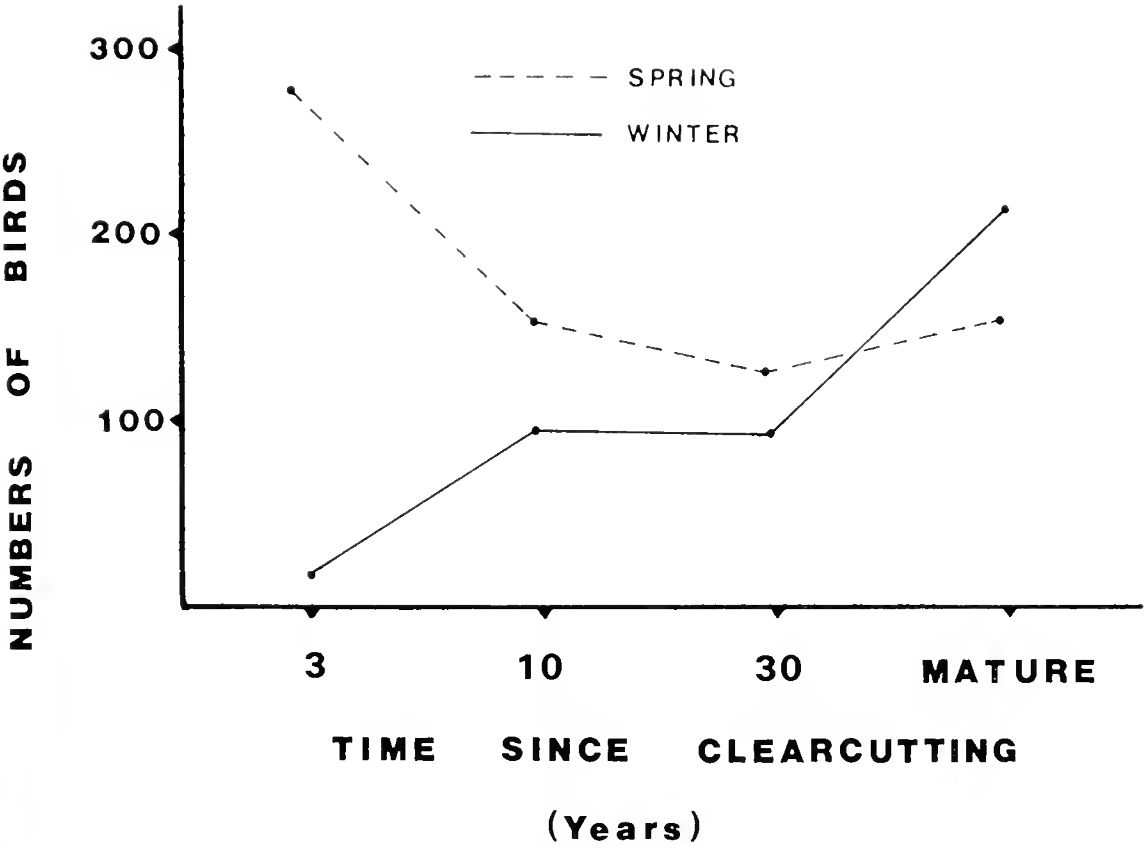

FIG. 6. Total number of birds seen or heard in the winter and breeding seasons.

tion showed an increasing trend (increasing evenness of bird species distribution) except for the 3-year-old area (Table 1).

Three-year-old clearcuts.—This area had the lowest winter bird species diversity (0.96) (Fig. 5), with a total of only 3 species (Table 1). A total number of 14 birds was seen in this area during the winter season (Table 1). Winter birds probably avoided this habitat condition because it did not provide the needed cover and food resources.

Ten-year-old clearcuts.—Carolina Chickadees (see Tables 1 and 2 for scientific names) and Golden-crowned Kinglets used this habitat condition regularly (Table 1). Red-breasted Nuthatches were also seen often. Winter bird species diversity was 1.82 (Fig. 5) and a total of 95 birds (Fig. 6) of 14 species (Table 1) was seen.

Thirty-year-old stands.—As in the 10-year-old clearcuts, Carolina Chickadees, Golden-crowned Kinglets, and Red-breasted Nuthatches were the most abundant species (Table 1). Winter bird species diversity was 1.87 (Fig. 5), and we observed a total of 90 birds (Fig. 6) of 11 species (Table 1).

Mature stands.—Black-capped Chickadees, Carolina Chickadees, Golden-crowned Kinglets, and Red-breasted Nuthatches occurred regularly in the mature stands. Red Crossbills and White-breasted Nuthatches were seen

TABLE 2

RELATIVE ABUNDANCE OF BIRD SPECIES IN THE 4 STUDY AREAS DURING THE BREEDING SEASON

Bird species	3-year-old clearcuts	10-year-old clearcuts	30-year-old stands	Mature stands
White-eyed Vireo (*Vireo griseus*)	0.007			
Great Crested Flycatcher (*Myiarchus crinitus*)	0.014			
Yellow-breasted Chat (*Icteria virens*)	0.069			
Field Sparrow (*Spizella pusilla*)	0.025			
Common Flicker (*Colaptes auratus*)	0.011	0.006		
Prairie Warbler (*Dendroica discolor*)	0.134	0.056	0.025	
Indigo Bunting (*Passerina cyanea*)	0.174	0.025	0.008	
Goldfinch (*Spinus tristis*)	0.080	0.125	0.085	
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.007	0.031	0.017	
Cardinal (*Cardinalis cardinalis*)	0.007		0.008	0.013
Hooded Warbler (*Wilsonia citrina*)	0.014	0.031	0.085	0.013
Gray Catbird (*Dumetella carolinensis*)	0.058	0.019	0.008	0.058
Rufous-sided Towhee (*Pipilo erythrophthalamus*)	0.322	0.406	0.144	0.213
Brown-headed Cowbird (*Molothrus ater*)	0.036	0.075	0.051	0.013
Carolina Wren (*Troglodytes ludovicianus*)	0.014		0.025	0.006
American Robin (*Turdus migratorius*)	0.014			0.006
Downy Woodpecker (*Picoides pubescens*)	0.007	0.013	0.017	0.019
Carolina Chickadee (*Parus carolinensis*)	0.004	0.088	0.127	0.168
Brown Thrasher (*Toxostoma rufum*)		0.013	0.017	
Cedar Waxwing (*Bombycilla cedrorum*)		0.013		
Blue Jay (*Cyanocitta cristata*)		0.006	0.059	0.026

TABLE 2 (continued)

Bird species	3-year-old clearcuts	10-year-old clearcuts	30-year-old stands	Mature stands
White-breasted Nuthatch (*Sitta carolinensis*)		0.006	0.017	0.006
Pine Warbler (*Dendroica pinus*)		0.025	0.076	0.142
Wood Thrush (*Hylocichla mustelina*)		0.006		0.032
Black-and-white Warbler (*Mniotilta varia*)		0.031	0.034	0.006
Blue-gray Gnatcatcher (*Polioptila caerulea*)		0.013	0.059	0.026
Tufted Titmouse (*Parus bicolor*)		0.006	0.042	0.019
Eastern Phoebe (*Sayornis phoebe*)			0.008	
Red Crossbill (*Loxia curvirostra*)			0.034	0.013
Acadian Flycatcher (*Empidonax virescens*)			0.017	0.006
Ovenbird (*Seiurus aurocapillus*)			0.025	0.097
Common Grackle (*Quiscalus quiscala*)			0.008	0.006
Pileated Woodpecker (*Dryocopus pileatus*)				0.013
Hairy Woodpecker (*Picoides villosus*)				0.019
Red-eyed Vireo (*Vireo olivaceus*)				0.026
Louisiana Waterthrush (*Seiurus motacilla*)				0.013
Common Crow (*Corvus brachyrhynchos*)				0.013
Scarlet Tanager (*Piranga olivacea*)				0.019
Yellow-billed Cuckoo (*Coccyzus americanus*)				0.006
Number of birds	276	160	118	155
Species diversity (H′)	2.16	2.19	2.83	2.64
Number of species (S)	18	21	24	27
Equitability (J′)	0.747	0.916	0.891	0.801

often (Table 1). Winter bird species diversity was the highest in the mature stands (2.34) (Fig. 5). We observed a total of 213 birds (Fig. 6) of 19 species (Table 1). The mature pine-oak forest apparently provided the best winter cover and food source of the 4 habitat conditions examined.

Breeding Season

No significant differences in breeding bird diversity were detected among the different aged pine-oak stands ($P \leqslant 0.05$). The 3-year-old clearcuts had a significantly higher total number of birds than any of the other stands ($P \leqslant 0.01$). The index of equitability (J') was higher in the intermediate stage of succession (10-year-old) when compared to the 3-year-old and mature stands. The highest index value occurred in the 10-year-old clearcut while the lowest was in the 3-year-old area (Table 2).

Three-year-old clearcuts.—Bird diversity and numbers were quite different during the breeding season from what they had been in the winter. Breeding bird species diversity was 2.16 (Fig. 5) with 18 species present (Table 2). A significantly greater number of birds (276) (Fig. 6) was seen in the 3-year-old clearcuts during the breeding season than in any of the other habitat conditions. Rufous-sided Towhees were extremely abundant in the 3-year-old clearcuts. Prairie Warblers, Indigo Buntings, American Goldfinches, and Yellow-breasted Chats were regularly observed (Table 2). The pines and dense deciduous growth apparently provided an abundant food supply and nesting sites for the bird species present.

Ten-year-old clearcuts.—Rufous-sided Towhees were the most abundant species in this habitat. American Goldfinches, Carolina Chickadees, Brown-headed Cowbirds, and Prairie Warblers were seen regularly (Table 2). Breeding bird species diversity (2.19) (Fig. 5) was similar to that observed in the 3-year-old clearcuts. A total of 160 birds (Fig. 6) of 21 species (Table 2) were seen in the 10-year-old clearcuts.

Thirty-year-old stands.—Rufous-sided Towhees and Carolina Chickadees were the most abundant species in the 30-year-old stands during the breeding season (Table 2). American Goldfinches, Hooded Warblers, and Pine Warblers were observed regularly. Breeding bird species diversity (2.83) (Fig. 5) and number of species (24) were higher in this habitat condition than in the 2 younger seral stages. However, the total number of birds seen (118) was the lowest of all the habitat conditions examined during the breeding season (Fig. 6).

Mature stands.—Rufous-sided Towhees, Carolina Chickadees, and White-breasted Nuthatches were the most abundant species in the mature stands (Table 2). Ovenbirds were seen regularly. Breeding bird species diversity in the mature stands (2.64) (Fig. 5) was lower than observed in the 30-year-old stands. The mature stands had the highest number of species (27) of all the areas; a total of 155 birds was seen (Fig. 6).

DISCUSSION

Breeding bird diversity and species richness in regenerating pine-oak clearcuts increased with age of the stand. This is similar to the pattern observed in other conifer stands by Johnston and Odum (1956) and Haapanen (1965). This pattern was not observed in oak-hickory clearcuts where breeding bird diversity and species richness were highest in stands 3 to 12 years old (Hooper 1967, Ambrose 1975, Conner and Adkisson 1975).

The equitability index was higher in the breeding season than in winter in all areas except the 3-year-old clearcut (Tables 1 and 2). The higher values during the breeding season are expected due to increased territoriality, and lack of the unpredictable and rigorous environment of the winter season (Tramer 1969, Kricher 1972). The higher equitability index of the 3-year-old area in winter could be due to the sparse bird life present as a response to limited cover. Similar results were found in Kricher's (1972) early successional stage in winter.

As the age of the pine-oak habitat increased, we also observed a change in breeding bird species composition. Early succession species like Indigo Buntings, Prairie Warblers, Common Flickers, Field Sparrows, Yellow-breasted Chats, and White-eyed Vireos that were present in the younger areas, became less abundant as the age of the area increased, and were totally absent from the mature pine-oak stands. Other species were associated mainly with the older stands: Pine Warblers, Red Crossbills, Ovenbirds, Pileated Woodpeckers, Hairy Woodpeckers, and Scarlet Tanagers. Successional changes in bird species composition with successional changes in vegetation have been reported for other geographical areas (Johnston and Odum 1956, Meslow and Wight 1975).

Several species of birds that occurred only in the more mature areas were negatively affected by pine-oak clearcutting. Pileated Woodpeckers favored the older stands in both the winter and breeding seasons. This preference is similar to that observed in oak-hickory stands (Conner and Crawford 1974, Conner et al. 1975). Red Crossbills depend on an abundance of mature cones as they feed extensively on pine seeds; this species appeared to prefer the more mature stands during both seasons and would probably be severely affected by clearcutting in any pine forest.

In winter as the age of the area increased, there was a trend for an addition of new bird species without the loss of species seen in the younger stands (Table 1). This was not a change in bird species composition as occurred during the breeding season (Table 2). Both total numbers of birds seen and bird species diversity in winter were severely reduced in the 3-year-old stands and gradually increased as the age of the area increased. From these observations, we concluded that pine-oak clearcutting reduced the capability of pine-oak habitat type to support winter bird populations.

Although bird species diversity was depressed, pine-oak clearcutting may have had a slightly beneficial effect on breeding bird populations of the total area being managed. In addition to a change in bird species composition between areas, there was a significant increase in numbers of birds in the 3-year-old clearcuts. This beneficial effect for breeding birds would probably only be realized if 2 conditions were met. Rotation time would have to be long enough to allow areas to reach 80+ years old to maximize the benefits to bird species that prefer a mature forest (Figs. 5 and 6). Rotation times this long are not economically beneficial for timber production in this timber type. Also, we speculate that a limitation may have to be put on the size of the area cut so that the entire area being managed is composed of many smaller subsets of different seral stages. Based on information in the literature, 10 ha is a large enough area to include most common species of birds in Georgia (Johnston and Odum 1956) and in mixed oak forests of New Jersey (Galli et al. 1976). Clearcuts no larger than 12–16 ha in size should be large enough to include most species of birds with the exception of those that have large home range requirements like the Pileated Woodpecker (at least 40 ha) (Tanner 1942).

Further research is needed to demonstrate the effects of even-aged management in other timber types. Eastern Bluebirds (*Sialia sialis*) nest in the younger regeneration stages of oak-hickory clearcuts (Conner and Adkisson 1974). We did not observe bluebirds in any of the pine-oak clearcuts even though the present study areas were in the same geographical area. Hairy Woodpeckers also foraged and nested in young oak-hickory clearcuts (Conner and Crawford 1974, Conner et al. 1975). In the present study, none were observed in the younger pine-oak clearcuts.

Pine-oak clearcutting can be beneficial or harmful to bird populations depending on the season, the seral stage, and the species of bird in question. If an area is to be managed under a multiple use policy, the factors concerning birds and other wildlife, in addition to timber needs, must be considered. There are always trade-offs in land management decisions; any management will have positive and negative effects. On viewing our results, we have concluded that the net effect of pine-oak clearcutting on birds in southwestern Virginia is negative.

SUMMARY

In pitch pine-oak stands in southwestern Virginia, winter species diversity and numbers of birds were lowest in the 3-year-old clearcuts and highest in the mature stands. Clearcutting reduced winter bird populations in all stages of pine-oak regeneration examined. There were no significant differences in bird species diversity among any of the study areas during the breeding season. The 3-year-old clearcuts had a higher number of birds during the breeding season than the other 3 differently aged areas. Species composition of breeding birds changed as the pine-oak stands regenerated toward maturity. When compared to the mature stands the net effect of pine-oak clearcutting on birds was negative.

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GENERAL NOTES

Experimental synchronization of sparrow reproduction.—This paper describes the results of attempts to synchronize the breeding activities of populations of House Sparrows (*Passer domesticus*) and European Tree Sparrows (*P. montanus*). The technique was first used to try to synchronize the breeding activities of House Sparrow populations so that hatching and the nestling period would coincide with peak emergence time of the 13-year periodical cicadas (*Magicicada* spp.) in order to test the effect of this superabundant food supply on reproductive success (see Anderson, Condor 79:205–208, 1977). The technique was also used to synchronize the breeding populations of both species in the same habitat in Poland so that the nestling diets of the 2 species could be compared at the same time within the same habitat and among nestlings of the same age. The nestling diets of the 2 species change markedly throughout the course of the prolonged breeding season (Anderson, Occ. Pap. Univ. Kans. Mus. Nat. Hist. 70, 1978) and with nestling age (Kalmbach, USDA Tech. Bull. 711, 1940; Grün, unpubl. Ph.D. dissert., Ernst-Moritz-Arndt-Univ., 1964). Although there is considerable overlap in the breeding seasons, particularly as the season progresses, the peak House Sparrow breeding begins 7–10 days before the European Tree Sparrow peak (Mackowicz et al., Ekol. Polska A 18:465–501, 1970).

The synchronization method consisted simply of removing the nest contents (eggs and/or nestlings) from all active nests on the same day. In the United States this was done on 4 May 1976, in 7 breeding colonies (some of which contained both species) in Missouri and Illinois near St. Louis, Missouri. In Poland the contents of nests were removed on 21 and 25 April and 27 and 28 May 1977, from nests in Dziekanów Lésny and Palmiry, near Warsaw. A description of that study area can be found in Pinowski (Ekol. Polska A 15:1–30, 1967). All nests in both studies were in nest-boxes.

I interrupted 140 (66 House Sparrow and 74 European Tree Sparrow) breeding attempts. In 48.6% of these nests, renesting occurred within 2 weeks of the interruption. In an additional 7.1% laying continued uninterrupted in nests where the clutch was not complete when interrupted. The desertion rate was therefore quite high (44.3%) and did not differ significantly between the species (House Sparrow 43.9%, European Tree Sparrow 44.6%, $P > 0.95$).

The desertion rate appeared to be affected by the availability of alternative nest-sites. Occupancy of nest-boxes ranged from 10 to 88.9% in different colonies. The desertion rate in the colony with 88.9% occupancy was only 20% while in the remaining colonies (average 26.3% occupancy) it was significantly higher (55.8%) ($P < 0.001$).

The mean interval between the interruption of 1 nesting attempt and the initiation of a new clutch in the same nest was 7.0 days (range 3–13, $s_{\bar{x}} = 0.47$) in the House Sparrow and 6.8 days (range 2–13, $s_{\bar{x}} = 0.38$) in the European Tree Sparrow. The difference was not significant ($t = 0.252$, $P > 0.80$). The House Sparrow had a strong mode of 7 days, and the European Tree Sparrow had a strong mode of 6 days (Fig. 1). Of the renesting efforts, 65.5% of the 29 House Sparrow clutches and 66.7% of the 39 European Tree Sparrow clutches were begun 6–8 days after the interruption.

The stage of the nesting cycle at which the nest was interrupted did not appear to have a consistent effect on either the interval between interruption and the initiation of a replacement clutch or on the desertion rate (Table 1). In the House Sparrow the interval was shortest in nests interrupted during egg laying, and was progressively longer in nests interrupted during the incubation and nestling periods. However, the differences

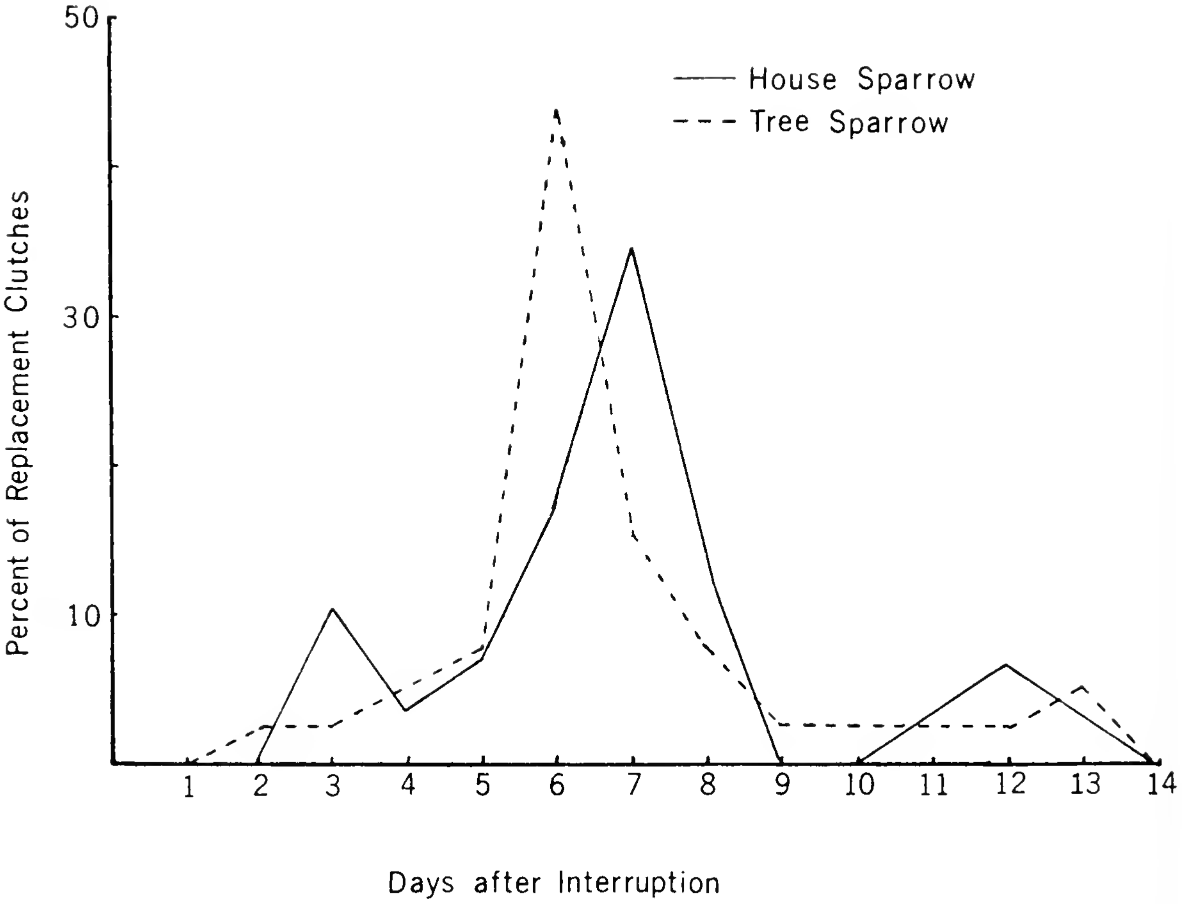

FIG. 1. Interval between interruption of breeding effort and initiation of a replacement clutch in House Sparrows and European Tree Sparrows.

were not significant ($P > 0.20$ in all cases). In the European Tree Sparrow the situation was reversed, with the longest interval being observed in nests interrupted during laying and progressively shorter intervals observed as the breeding cycle continued. The difference between the interval for nests interrupted during laying and those interrupted during the feeding of nestlings was, however, the only significant difference ($t = 2.424$, $P < 0.05$).

The highest desertion rate in the House Sparrow was from nests interrupted during incubation, while the lowest rate was observed in nests interrupted during laying. The difference was significant ($\chi^2 = 9.821$, $P < 0.01$). In the European Tree Sparrow the highest desertion rate was observed in nests interrupted during the nestling period, but the differences between stages were not significant.

The data were insufficient to analyze for intercontinental differences in desertion rates and intervals before renesting in the 2 species, but there were no apparent differences between continents.

The synchronization techniques proved basically successful. The high percentage of birds that initiated a replacement clutch 6–8 days after the interruption of their initial breeding effort was particularly significant. The use of alternative sites in sparsely populated colonies, with a similar interval between the interruption and the initiation of a second clutch, further increased the effectiveness of the technique. The technique might

TABLE 1

DESERTION AND RENESTING RATES AND INTERVALS TO RENESTING OF HOUSE SPARROWS AND EUROPEAN TREE SPARROWS AFTER INTERRUPTION OF ACTIVE NESTS, ACCORDING TO STAGE OF NESTING CYCLE AT TIME OF INTERRUPTION

Species	Nesting stage	N	% deserted	% continued	% renested	Intervals in days ($s_{\bar{x}}$)
European Tree Sparrow	Laying	37	35.1	5.4	59.5	7.4 (0.64)
	Incubation	14	35.7		64.3	6.3 (0.17)
	Nestling	23	65.2		34.8	5.6 (0.32)
	Total	74	44.6	2.7	52.7	6.8 (0.38)
House Sparrow	Laying	16	12.5	50.0	37.5	5.5 (1.36)
	Incubation	24	62.5		37.5	7.0 (0.71)
	Nestling	26	46.1		53.8	7.6 (0.60)
	Total	66	43.9	12.1	43.9	7.0 (0.47)

be successfully used in a number of experimental situations where synchronization of breeding in free-living sparrow populations is desirable.

The applicability of the technique to other bird species is questionable. Most open-nesting species desert their nest after a nest failure and, if they renest, construct a new nest at a different site. Other hole-nesting species, which use a nest-site that affords more protection than an open site (Nice, Auk 74:305–321, 1957) and that is frequently in short supply (von Haartman, pp. 391–459 *in* Avian Biology, Vol. I, D. S. Farner and J. R. King, eds., Academic Press, New York, 1971), may be less prone to desert their nest-site after a failure, although I have no data to support this suggestion. The response of the 2 sparrow species may represent an adaptation to their commensal relationship with man. Persistence in attempting to nest in a favorable site in spite of active interference by man may be selectively advantageous.

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Sexual differences in feeding territoriality of the Crowned Woodnymph, *Thalurania colombica*.—We observed territorial behavior of an adult male and female Crowned Woodnymph (*Thalurania colombica*) on 27, 28, 29 June and 2 July 1977, near the Limbo Hunt Club on Pipeline Road, Gamboa, Canal Zone. Sexing and aging followed Ridgway (U.S. Natl. Mus. Bull. 50, Pt. V, 1911). The female defended a smaller, higher quality territory than did the male and was more aggressive in defense, unlike other species of hummingbirds (Wolf and Hainsworth, Ecology 52:980–988, 1971; Linhart, Am. Nat. 107:511–523, 1973; Stiles, Univ. California Publ. Zool. 97:1–109, 1973).

The female defended a large *Hamelia patens* (Rubiaceae) bush 16 m^2 in cross section, bearing 280–325 open flowers per day. The male's territory of roughly 200 m^2 included an *Hamelia* bush with about 30 flowers, several flowering *Heliconia* (Musaceae) and 1 or 2 flowering *Gustavia* sp. (Lecythidaceae). Both birds occasionally visited small *Hamelia* plants outside their territories, which were about 200 m apart.

More intruders visited the female's territory than the male's. The female made 30 chases in 345 min of observation (1 per 12 min) while the male made 3 chases in 325 min (1 per 108 min). Chases by the female were more aggressive than those by the male, often involving rapid pursuit and high-pitched calling. Chases by the male mostly involved displacement, with the intruder leaving when approached. Intruders sometimes fed unmolested in the male's territory, probably because the male did not see them due to the territory's large size. Intruders in the female's territory were usually chased before they could feed, or fed only for a few sec before being discovered. The female often chased butterflies (yellow-orange pierids and *Heliconius* sp.) which appeared to be feeding from *Hamelia* flowers, while the male chased only 1 butterfly. Hummingbird intruders in the male's territory included Long-tailed Hermits (*Phaethornis superciliosus*), male Crowned Woodnymphs and a Blue-chested Hummingbird (*Amazilia amabilis*), and in the female's territory Blue-chested Hummingbirds and at least 1 female Crowned Woodnymph.

The mean nectar volume of *Hamelia* flowers in the female's territory was 2.4 μl ($N = 60$, $SD = 1.7$) and the mean volume in the male's territory was 0.4 μl ($N = 60$, $SD = 0.4$). Nectar volume of *Hamelia* flowers in the female's territory was significantly greater than that in the male's territory (Table 1). Nectar content of *Gustavia* and *Heliconia* was not quantified, and we assumed that nectar availability of *Hamelia* would roughly reflect its availability throughout the territory.

Intruder frequency, intensity of aggression, territory size and nectar content of *Hamelia* flowers suggest that the female's territory was of higher quality than was that of the male. Feinsinger and Chaplin (Am. Nat. 109:217–224, 1975) suggested that hummingbird food exploitation patterns are related to wing disc loading and that

TABLE 1

NECTAR VOLUMES OF *HAMELIA* FLOWERS IN TERRITORIES OF MALE AND FEMALE *THALURANIA COLOMBICA*

		Nectar volume per flower (μl)	
Date	Time	Male	Female
27 June	08:00	0.2[1]	5.8[1]
27 June	11:20	0.0	2.2
28 June	06:50	0.3	1.2
28 June	10:30	1.2	1.6
29 June	06:40	0.5	1.4
02 July	15:20	0.3	2.3
$t = 2.58$	$P < 0.05$[2]		

[1] Values are means of 10 flowers.

[2] t value determined using paired comparisons test.

sexes or species with higher loadings are usually more territorial than are those with lower loadings. A sample of 16 male and 5 female woodnymphs from nearby Barro Colorado Island showed no significant loading differences (0.030 and 0.031, respectively, $P > 0.05$), although this difference is little less than that between sexes of some territorially dimorphic species reported by Feinsinger and Chaplin (Am. Nat., op. cit.).

Further observations are needed to show whether the observed behavioral differences are typical of the species and whether there is a real difference in wing disc loading between the sexes.

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Brown-headed Cowbird parasitism on Eastern Bluebirds.—Brown-headed Cowbirds (*Molothrus ater*) infrequently lay their eggs in nests of Eastern Bluebirds (*Sialia sialis*). In the most recent compilation (Friedmann et al., Smithson. Contrib. Zool. No. 235, 1977), only 49 records are listed. Musselmann (Bird-Banding 17:60–73, 1946) recorded the highest rate of brood parasitism when, in 1945, he found cowbird eggs in 7 of 268 (2.6%) active bluebird nests in Illinois nest boxes. This note reports on a small population of Eastern Bluebirds that has been subjected to a relatively high rate of cowbird parasitism.

Since spring 1974, from 11 to 14 nest boxes have been maintained for bluebirds on the grounds of the U.S. Geological Survey National Center and adjacent residental areas in Reston, Virginia. The population has increased from 2 pairs in 1974 to 6 pairs in 1976 and 1977. During these 4 years, 6 of 27 (16.2%) bluebird nests with completed clutches were parasitized by cowbirds. Another 3 bluebird nests were almost completely built, but no eggs were laid. Of these, a cowbird laid an egg in 1 nest, giving an overall parasitism rate of 17.5%. Yearly rates were 0% in 1974, 30% in 1975, 16.9% in 1976, and 14.3% in 1977 ($\bar{x} = 15.25$).

Besides bluebirds, Carolina Chickadees (*Parus carolinensis*) nested in the boxes once and Carolina Wrens (*Thryothorus ludovicianus*) nested thrice. One of the wren nests was parasitized, and 2 cowbirds, but no wrens, fledged.

There were 2 periods of cowbird activity—1 in late April to early May and 1 in June—corresponding to the 2 main bluebird nesting periods. Five of the parasitized nests, including the 1 without bluebird eggs, were first nestings, 1 was a second nesting, and 1 in June may have been a first nesting, or possibly a renesting, but this could not be confirmed.

One or 2 ($\bar{x} = 1.43$, $N = 7$) cowbird eggs were laid in each parasitized nest. Judging from nest checks during egg-laying and incubation, the female cowbirds did not remove any bluebird eggs.

Data were sufficient to determine accurately the outcome of 4 parasitized nests. Two of these nests produced no cowbirds—1 because the cowbird laid an egg in an already deserted nest and 1 because the egg was laid 1–3 days before the bluebird eggs hatched. In the other 2 nests, 3 cowbirds but no bluebirds fledged. The cowbird eggs hatched at least 1–3 days before the bluebird eggs, thus giving a competitive advantage over the young bluebirds, which appeared to die from starvation. In 1 nest, an almost dead nestling bluebird was still present when 2 cowbirds fledged.

In the 3 remaining parasitized nests, cowbird eggs or young were removed for another study; however, it is possible to determine the probable outcome of 2 of these nests based on the embryonic development of an egg when collected compared to the hatching date of the bluebird eggs in 1 and the time interval between hatching of a cowbird egg and the bluebird eggs in the other. In the first case, the cowbird egg would not have hatched. In the other case, a cowbird, but not the bluebirds, would have fledged. Bluebirds fledged from all 3 of these nests after the cowbird eggs or young were removed. In the 2 cases where only cowbirds fledged and in the other case where probably only cowbirds would have fledged, the parasitized bluebird pairs also produced a brood of their own at some other time in the same breeding season.

Of the 3 cowbirds that fledged from these nest boxes, 1 was raised to independence and 2 (from the same nest) were presumably taken by a predator within a day of fledging. Besides these records, from 29 May to 1 June 1974, we saw a female bluebird feeding a fledgling cowbird in the area but saw no young bluebirds. Friedmann (U.S. Natl. Mus. Bull. 233, 1963) reported no records of Eastern Bluebirds rearing Brown-headed Cowbirds.

There are 2 probable reasons for the relatively high rate of cowbird parasitism in this Eastern Bluebird population—nature of the nest boxes and population density of potential hosts. The boxes were made from cardboard, half-gallon cartons (Woodward, Md. Birdlife 29:151–152, 1973), and no effort was made to cut openings to an exact size. As a result, openings of these were considerably larger ($\bar{x} = 5.4$ cm, $N = 25$) than that recommended (3.8 cm [1.5 in.]) by Zeleny (The Bluebird, Indiana Univ. Press, Bloomington, 1976). Thus female cowbirds could easily enter the milk cartons while it would be difficult or impossible for them to enter a smaller opening. This is similar to the situation Musselmann (op. cit.) found in 1945 when all of his 7 parasitized nests were in nest boxes where the roofs had been removed for a time.

These boxes are also quite conspicuous, making them easy to find by cowbirds. The fact that an egg was laid in a deserted nest suggests that at least in some cases female cowbirds find nests without observing adult hosts near the nest. However, this cannot be the only explanation because the same type of box is used at McKee-Beshers Wildlife Management Area, Maryland, about 16 km from Reston. Yet, from 1971 to 1977, none of 120 bluebird nestings in these boxes was parasitized.

Compared to McKee-Beshers, which is on the Potomac River floodplain and has a wide variety of habitats and a high density of breeding birds (pers. obs.), the area where bluebirds nest in Reston is a mostly uniform habitat of upland forest and lawns and has a relatively low density of breeding birds. Of the most recent 52 breeding bird censuses from eastern deciduous forests (reported in American Birds 31:24–93, 1977), only 7 had a lower density than the forest in Reston (see census No. 32). The grounds of the National Center also have a low density of breeding birds, especially of potential hosts (pers. obs.), so cowbirds may have been limited to laying their eggs in bluebird nests, whereas at McKee-Beshers, cowbirds have a much wider choice of hosts.

We thank E. S. Morton for comments on a draft of this note and the U.S. Geological Survey, particularly Philip Cohen, for assistance and for permission to work at the National Center.—PAUL W. WOODWARD, *Dept. of Zoology, Univ. of Maryland, College Park, Maryland 20742, and* JOAN C. WOODWARD, *2433 Southgate Sq., Reston, Virginia 22091.* *Accepted 21 Apr. 1978.*

Wilson Bull., 91(2), 1979, p. 323

Interspecific use of Sandhill Crane nests.—Sandhill Crane (*Grus canadensis tabida*) nesting studies have been in progress in southeast Oregon since 1966. More than 650 nests have been examined, and 4 of these nests have contained eggs of other species. After eggs have hatched or have been destroyed, many crane nests are used by waterfowl and marsh birds for loafing sites. The following are the only instances I have recorded of interspecific use of crane nests for egg deposition.

On 13 May 1976, a nest was located 5 km south of Burns, Harney Co., Oregon. It contained 2 crane eggs and 1 Canvasback (*Aythya valisineria*) egg. The nest was both built in and composed of broad-fruited burreed (*Sparganium eurycarpum*). The Canvasback egg was next to the crane eggs and was apparently being incubated by the cranes. The Canvasback egg was collected and the 2 crane eggs hatched in early June. Johnsgard (Waterfowl of North America, Indiana Univ. Press, 1975) mentioned that Canvasback socially parasitize other females of their own species and have been known to lay eggs in the nests of both Redheads (*Aythya americana*) and Ruddy Ducks (*Oxyura jamaicensis*). I know of no other record of Canvasback egg parasitism of species other than waterfowl.

In southeast Oregon, Canada Geese (*Branta canadensis moffitti*) nest at the same time as Sandhill Cranes and use similar habitat. A crane nest that was lost to an unknown predator contained 2 goose eggs when re-examined on 12 April 1969. The goose eggs had apparently been deposited in the nest after the crane eggs had been destroyed; they had not been incubated. On 11 April 1974, a deserted crane nest with 2 crane eggs and 5 Canada Goose eggs was located. All 7 eggs had been covered with nesting material. Normally, Sandhill Cranes do not cover the eggs until they have been destroyed or hatched (shell fragments). Both of these nests were located on Malheur National Wildlife Refuge, about 50 km southeast of Burns.

An active nest was located on Malheur NWR in April 1971. When re-examined in May it was occupied by a Trumpeter Swan (*Olor buccinator*). The swan had added material to the nest and was incubating 5 swan eggs. Fate of the crane eggs was not determined, but the swan eggs hatched successfully. The crane eggs had probably been destroyed before the swan added material to the nest.

I would like to thank Caryn E. Talbot for reviewing a draft of this note; and Lewis Oring for refereeing the manuscript.—CARROLL D. LITTLEFIELD, *U.S. Fish and Wildlife Service, Box 671, Burns, Oregon 97720. Accepted 11 May 1978.*

Wilson Bull., 91(2), 1979, pp. 323–328

The Red-whiskered Bulbul in Hawaii.—The Red-whiskered Bulbul (*Pycnonotus jocosus*) is native to India, but has been introduced into Australia (Chaffer, Emu 33:136–137, 1933; Barrett, Australian Bird Life, Brown, Prior, Anderson Pty., Ltd., Melbourne, 1947), Florida (Banks and Laybourne, Auk 85:141, 1968; Owre, Wilson Bull. 85:491–500, 1973), and Hawaii. In both Australia and Florida the bird is well established and has become somewhat of an agricultural pest. This bulbul was first recorded in the lower Makiki Heights area of Oahu in 1965 (Kjargaard, Elepaio 29:35, 1968). Over a 10-year period following their establishment, the birds have been reported only in small numbers (Table 1). However, since 1967 the species has spread

TABLE 1

THE NUMBER OF RED-VENTED AND RED-WHISKERED BULBUL SIGHTINGS ON OAHU, HAWAII*

	Year											
Species	65	66	67	68	69	70	71	72	73	74	75	76
Red-whiskered Bulbul	0	0	2	7	0	0	4	0	0	2	5	77
Red-vented Bulbul	0	0	0	9	7	7	26	56	14	50	212	453

* Number of birds observed in annual Christmas counts by the Hawaii Audubon Society.

to Pacific Heights (Pyle, Elepaio 28:69–71, 1968), and we have recorded a range expansion and population explosion throughout the length of Manoa Valley (Fig. 1). This restricted expansion is in marked comparison to the Red-vented Bulbul (*Pycnonotus cafer*) which arrived in Hawaii at approximately the same time and has spread over a much wider region of Oahu (Fig. 1). Berger (Elepaio 36:16–19, 1975) believed multi-introductions were responsible for the wide distribution of the latter species.

Feeding habits.—A plethora of fruit-bearing trees have been imported to Hawaii, and many thrive in the lowland residential districts of Oahu (Neal, Bernice P. Bishop Mus., Special Publ. 50, 1965). These trees have supplied bulbuls with a wide variety of fruits, of which some type is almost always present at any given time of year. Red-

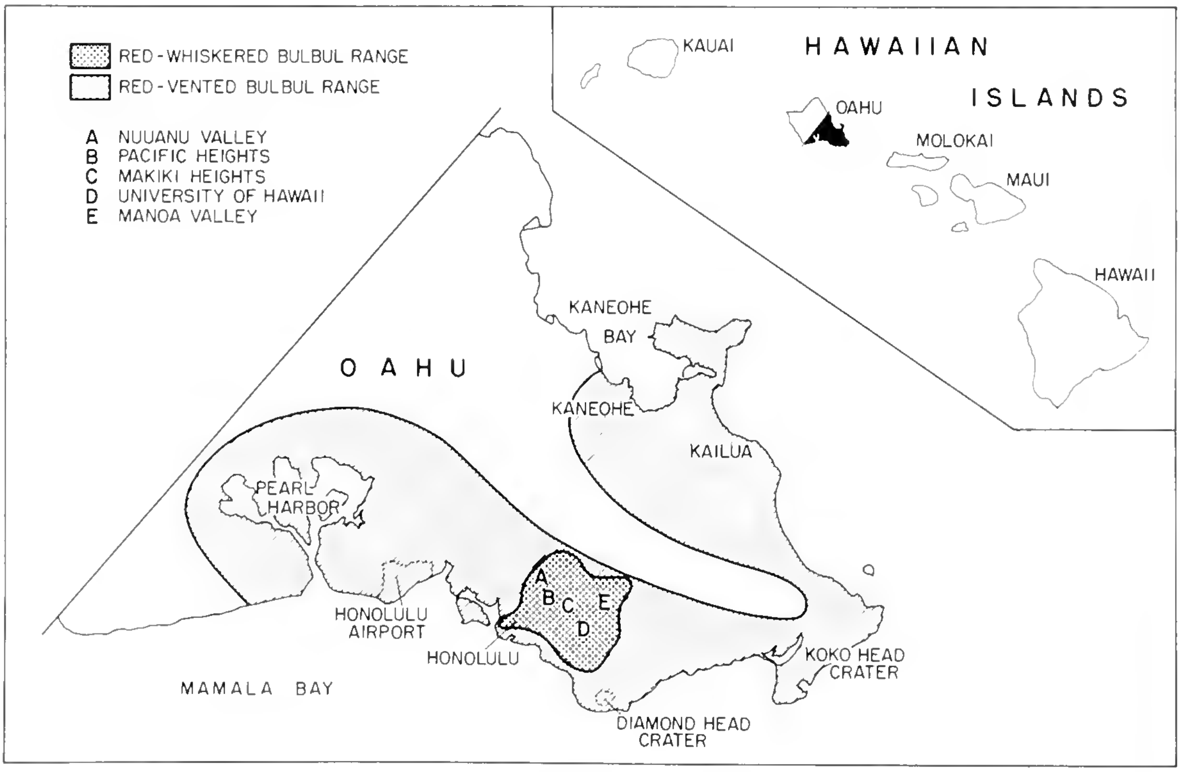

FIG. 1. Distribution of Red-whiskered and Red-vented bulbuls on Oahu, Hawaii.

whiskered Bulbuls have been reported feeding on the date palm (*Phoenix dactylifera*) (Roberts, Elepaio 30:66, 1970). We have observed its favorite fruits to be papaya (*Carica papaya*), mango (*Magnifera indica*), the fruits of the autograph tree (*Clusia rosea*), and berries of the several banyan (*Ficus*) species present here. It also fed on loquat (*Eriobotrya japonica*), avocado (*Persea americana*), and fruits of the octopus tree (*Brassaia actinophylla*) when these fruits were in season. Berries from mock orange (*Murraya exotica*) were readily taken as were fruits from many species of introduced palms.

Carleton and Owre (Auk 92:40–57, 1975) listed numerous fruits eaten by the Red-whiskered Bulbul in Florida, and indicated that the birds were incapable of piercing the skin of citrus and other large fruits, eating these only after another species of animal had created an opening. This was apparently only true for mature avocado in Hawaii, for the bulbul could pierce the skin of all other listed food items. It may be that as these fruits became overripe, the skin tore and birds enlarged the opening.

Bulbuls in Hawaii also ate nectar, a variety of insects, and possibly smaller reptiles. Thomson (A New Dictionary of Birds, McGraw-Hill Book Co., New York, 1964) cited nectar feeding in bulbuls, and Carleton and Owre (op. cit.) reported that captive birds exhausted containers of sugar-water solution faster than ones of plain water. In Hawaii the bottle brush (*Callistemon lanceolatus*) and coconut palm (*Cocos nucifera*) were the 2 primary nectar sources used by bulbuls. The birds also gathered insects from a variety of substrates in many different fashions. The most common technique of capture was short flights from perches, although the birds often gleaned up and down tree trunks. Possibly because numbers are still low in Hawaii, the degree of insect gathering at roosts reported by Meriwani (Ibis 115:285, 1973) and Carleton and Owre (op. cit.) was not observed. Birds also used corners of buildings that had large spider webs, hovering in front and plucking insects out. Another preferred substrate was roofs of larger buildings; birds walked along the gutter and frequently were observed running up the roof in pursuit of insects they had flushed. On 3 August 1977, a bulbul was observed chasing a large (ca. 20 cm in length) chamelion (*Anolis* sp.) in a circular pattern down an octopus tree; it was unsuccessful in capturing the reptile.

Nesting.—Prior to the population explosion in 1976, virtually nothing had been reported on the nesting habits of the Red-whiskered Bulbul in Hawaii. Roberts (Elepaio 32:9, 1971) told of a pair fledging 1 young on 20 April. The nest was 1.5 m above ground and located in a croton (*Codiaeum variegatum*) hedge. Apparently the pair built another nest in the same location and fledged 2 more young on 14 August 1971 (Roberts, Elepaio 32:38, 1971). Ohashi and Ueoka (Elepaio 38:1, 1977) reported in May on 3 nests in upper Makiki. They gave measurements of the nests and of 1 egg. Morgan (pers. comm.) found a pair nesting in upper Nuuanu during May 1977. Berger (Elepaio 38:35–38, 1977) summarized other records.

In 1973 there was apparently only 1 resident pair on the University of Hawaii campus, while in the past year (1977) numerous birds were present. In a small section of campus (35 ha), 2 pairs successfully nested. The Red-whiskered and Red-vented bulbuls seemed to "partition" this study area and there appeared to be little interspecific territory overlap. This may have been a sampling artifact, or it may indicate some degree of competitive exclusion as the 2 species do have similar diets (Ali and Ripley, Handbook of the Birds of India and Pakistan, Vol. 6, Oxford Univ. Press, Bombay, 1971).

On 19 April 1977, a pair of Red-whiskered Bulbuls was discovered constructing a nest. The structure was partially completed, located 3.6 m from the ground in an up-

FIG. 2. Red-whiskered Bulbul nestlings on day 3.

right terminal fork of a jasmine (*Trachelospermum jasminoides*) hedge. Birds brought material to the nest throughout the initial day of discovery and the next; tissue paper and strands of bark adorned the outside of the cup.

On 22 April 1977, the nest contained 2 eggs. These had a white background with dark

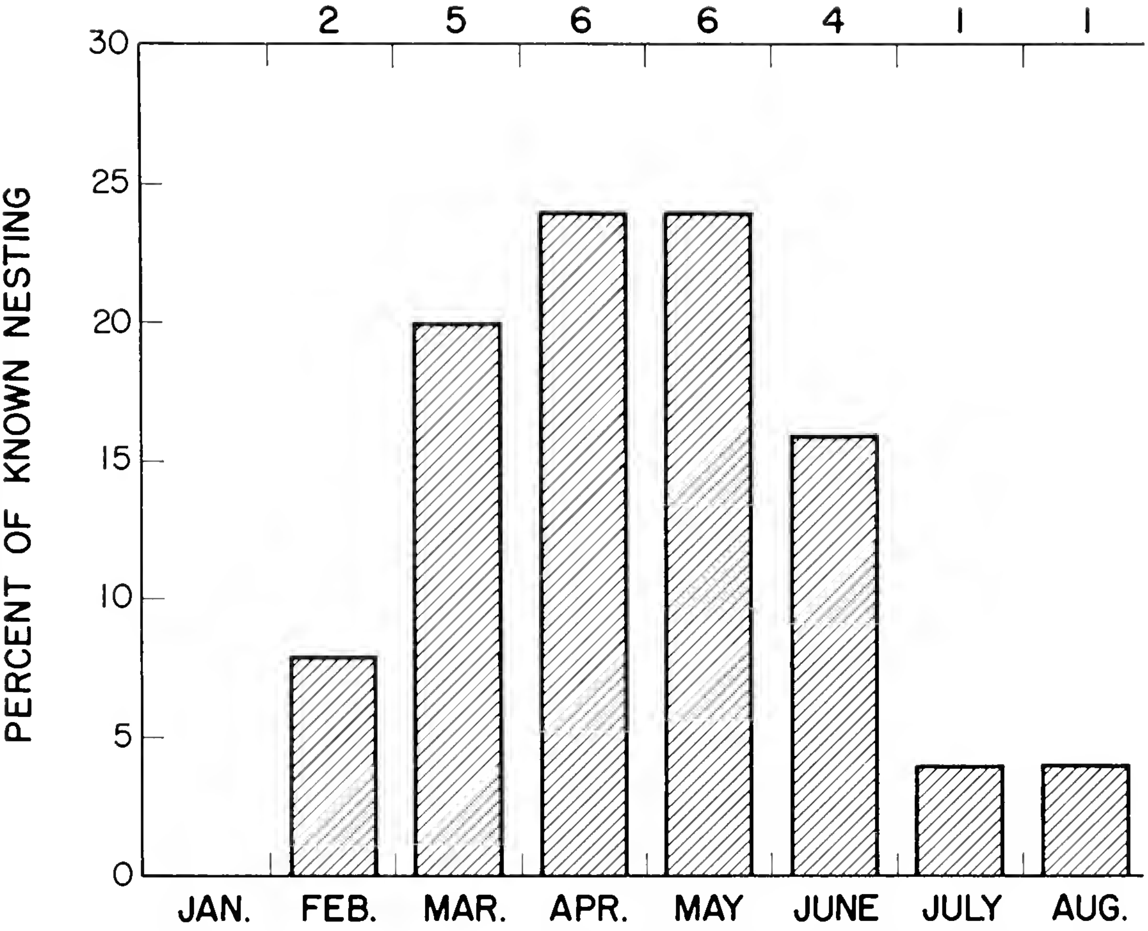

FIG. 3. Breeding season of the Red-whiskered Bulbul in Hawaii. Numbers are nests known to be active during that month. No nesting is recorded from September through December.

brown splotches of varying sizes that covered the surface, but were concentrated at the larger end. On 2 and 3 May, a bird was incubating 3 eggs. At 15:40 on 4 May, 2 young had hatched and the remaining egg was pipped. The third egg hatched that evening; early the next morning 3 young were active in the nest and readily gaped when the nest was moved. Assuming consecutive days of egg-laying and incubation, the incubation period was 11 days.

The young were naked at hatching. On 7 May, the nestlings were in pin feathers, their eyes had not yet opened, and they still gaped when the nest was shaken (Fig. 2). Their mouth lining was red on the outside and blended to yellow in the middle. Only the posterior half of the rictus (to the commissural point) was bright white. On 14 May, 2 young remained in the nest and were fully feathered. At 14:00 on 16 May, both young were present but perched on the nest rim. They apparently fledged that afternoon as the nest was empty the following morning at 07:00. The nestling period was 12 days.

The used nest was collected in August and had not been reused. Nest measurements were as follows: nest height was 8 cm; nest width varied from 8 to 10 cm; bowl depth was 5 cm; bowl width varied from 6 to 7.5 cm; and nest weight was 9.9 g. The nest had a leaf base with coarse grass and flexible stems of small shrubs woven together to make a bowl; there was no cup lining. The exterior was adorned with tissue paper, pieces of wide grass, and strips of bark.

Breeding season.—The breeding season of the Red-whiskered Bulbul in India is "chiefly March to July in the north, December to June in the south with a second period in September after the monsoon" (Ali and Ripley, op. cit.). Carleton and Owre (op. cit.) reported their earliest nest on 9 February. From data presently available, an extended breeding season seems also to be the case in Hawaii (Fig. 3). One bulbul was observed carrying nesting material as early as 29 February 1976 (pers. obs.); young were reported to have fledged as late as 14 August 1971. With an equable climate throughout the year, and release from competition, it is not surprising to find a protracted breeding season in Hawaii.

The first author was supported by World Wildlife Fund Grant US-35 and The Frank M. Chapman Memorial Fund during these field observations, and by a National Park Service Contract No. CX 8000 7 0009 during preparation of the manuscript. We thank T. Nakata for preparation of the figures and D. Weiner for typing the manuscript. R. Barbee, D. Reeser, and C. W. Smith provided logistical support.—CHARLES VAN RIPER, III, *and* SANDRA G. VAN RIPER, *Avian Disease Laboratory, Univ. of Hawaii Cooperative National Park Resources Studies Unit, P.O. Box 54, Hawaii Volcanoes National Park, Hawaii 96718, and* ANDREW J. BERGER, *Zoology Dept., Univ. Hawaii, Honolulu, Hawaii 96822.* *Accepted 11 Feb. 1978.*

Wilson Bull., 91(2), 1979, p. 328

Removal of fur from a live raccoon by Tufted Titmice.—We have raised and released a number of raccoons (*Procyon lotor*) into the wooded property at the back of our home. Although the raccoons are self-sufficient in the wild they tend to return to the vicinity of our home at fairly regular intervals. During the spring of 1976 1 individual chose to rest high in the limbs of a shingle oak (*Quercus imbricaria*) during the afternoons.

On 3 separate occasions between mid-April and the first week of May we observed a pair of Tufted Titmice (*Parus bicolor*) obtaining nesting material from the back of a raccoon. Typically, a pair of birds would fly to some branches next to the raccoon. Then, as 1 bird sat on a branch watching, the second individual made continuous short flights to the tail and more rarely the back of the raccoon pulling out small amounts of underfur. At times the bird perched directly on the back of the raccoon. The titmouse had to retreat quite often since the raccoon would finally become so annoyed that it would swipe at the bird with its forepaw or snap at it. However, the titmouse was never discouraged for long and simply resumed its efforts until its beak was full of fur. Then it would fly off to the nest to deposit the fur. At other times the 1 titmouse collecting fur transferred it to the watching partner and once both bills were full they would fly off together in the direction of the nest. Eventually, the titmice would return to the raccoon and this occurred several times during each observation period. Reports in the literature document the fact that the titmouse is an opportunist and collects nesting material from other living animals including the red squirrel (*Tamiasciurus hudsonicus*), woodchuck (*Marmota monax*), and opossum (*Didelphis virginiana*) (see J. W. Goertz, Wilson Bull. 74:189–190, 1962).—BARBARA K. ESHBAUGH, *Oxford, Ohio 45056 and* W. HARDY ESHBAUGH, *Dept. of Botany, Miami Univ., Oxford, Ohio 45056.* *Accepted 19 May 1978.*

Wilson Bull., 91(2), 1979, p. 329

Pomarine Jaeger preys on adult Black-legged Kittiwake.—On 5 June 1977, while on a cruise in the decomposing pack ice in the Bering Sea, we observed a light phase Pomarine Jaeger (*Stercorarius pomarinus*) attack, kill and feed on an adult Black-legged Kittiwake (*Rissa tridactyla*), 1 of approximately 10 individuals within 20 m of the ship's stern. We did not observe the birds until 1 min after the initial attack and do not know if the kittiwake was sitting or flying. No food was visible in the kittiwake's bill at the start of our observations nor was it observed regurgitating its stomach contents after the attack. During the first 5 min the kittiwake managed to become airborne a number of times but the jaeger maintained its hold and forced it back to the water. After 5 min the jaeger began to submerge the kittiwake's head, still holding it by the neck. Because of the kittiwake's struggling, the jaeger was unable to hold it under for more than 5 sec at a time. For the next 15 min it continued to submerge the victim's head, lift it out of the water, and then submerge it again. When it held the kittiwake under water, it kept both feet on its lower neck; this may have helped keep the head submerged. In the last 5 min of this activity, when the kittiwake offered little resistance, the jaeger occasionally used only its feet to push it under water. Other kittiwakes remained in the area, a few swimming within 2 m of the 2 birds. No attempt was made to mob the jaeger.

When the kittiwake appeared lifeless the jaeger turned it over, tore at the feathers and skin just below the sternum and opened a hole. It then began to feed while sitting beside the kittiwake. Although it was within 1 m of ice cakes it made no attempt to carry the kittiwake to the ice. We watched the jaeger feed for approximately 10 min before approaching and examining the kittiwake which had no wounds on the neck and head, indicating that death occurred by drowning or shock. The liver and intestine had been removed and the jaeger had just begun to eat the breast muscle.

While jaegers are known to be predators on birds, this is most frequently observed in Parasitic Jaegers (*S. parasiticus*) which hunt in pairs on the tundra and prey on birds as large as ptarmigan (*Lagopus* sp.) (Maher, Pac. Coast Avif. 37:107–115, 1974; Eisenhauer and Paniyak, Auk 94:389–390, 1977). Pomarine Jaegers have been observed feeding on phalaropes (Phalaropodidae) at sea (Bent, U.S. Natl. Mus. Bull. 113:11, 1921) but there are no previous records of it preying on large birds.

Little prey was available to surface-feeding birds in the area. The stomachs of most surface-feeding birds collected during the cruise were empty and densities of all surface-feeding birds were low. Maybe the inability of the Pomarine Jaeger to obtain fish or zooplankton directly or by piracy forced it to prey on a species it normally parasitizes.

This study was supported by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration, under which a multi-year program responding to needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) Office. This is Contribution Number 160 of Point Reyes Bird Observatory.—George J. Divoky, Karen L. Oakley *and* Harriet R. Huber, *Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970.* *Accepted 24 June 1978.*

Wilson Bull., 91(2), 1979, p. 330

Black-billed Magpie Predation of a Killdeer Nest.—On 6 June 1975, I observed a group of 6 adult Killdeer (*Charadrius vociferus*) vocalizing and displaying near a Black-billed Magpie (*Pica pica*). Their behavior was similar to the "mobbing" behavior described by Phillips (Anim. Behav. 20:1–9, 1972). Four of the birds stood in sleek or fluffed upright postures, moving occasionally as the magpie hopped among them. The other 2 birds frequently assumed "false brooding" postures, settling on the ground as if incubating, then moving and resettling when the magpie approached them. The magpie hopped back and forth among the Killdeer, stopping occasionally for 1–2 sec and cocking its head from side to side as if inspecting the ground. This behavior continued for 14 min.

One of the Killdeer that had been false brooding then attacked the magpie, flying at it from behind and attempting to beat its wings against the magpie's head and back. The magpie hopped a few cm in the opposite direction, keeping its head pointed toward the attacking Killdeer; it then hopped in its original direction pausing to fend off 2 similar attacks made by the same Killdeer. Finally, it picked up an egg in its beak and flew out of sight to the south accompanied by a juvenile Black-billed Magpie that had been standing approximately 60 m from the Killdeer nest. After 10 min, 5 of the Killdeer dispersed and 1 returned to incubate the remaining eggs.

Thirty min later a magpie flew back from the south. Again 6 Killdeer converged near the nest and joined the incubating Killdeer in displaying near the magpie. The Killdeer attending the nest made 2 attacks on the magpie but within 5 min the magpie found the nest and flew out of sight to the south with a second egg. Following this encounter the nest was left unattended. One h later a magpie flew back from the south, landed less than 1 m from the nest and removed a third egg. I then inspected the nest and found that 1 egg remained. The nest was empty when I returned the next morning.—John T. Mundahl, *Dept. of Biology, Utah State Univ., Logan, Utah 84322. (Present address: College of Veterinary Medicine, Univ. of Minnesota, St. Paul, Minnesota 55108.)* *Accepted 1 Mar. 1978.*

Wilson Bull., 91(2), 1979, pp. 330–331

Opportunistic feeding on man-killed prey by Ferruginous Hawks.—On 24 September 1977, while I was using a rifle to collect black-tailed prairie dogs (*Cynomys ludovicianus*) 10 km east of Hayden, Union Co., New Mexico, a Ferruginous Hawk (*Buteo regalis*) appeared and alighted near my vehicle. This occurred after several shots had been fired. Within 10 min the bird was joined by 4 more Ferruginous Hawks. These birds also landed and their positions, along with that of the original hawk, outlined a rough semicircle (with a 35-m radius) that was centered on my vehicle. The hawks were spaced at ca. 25-m intervals. When a prairie dog was shot in the general vicinity of 1 of the hawks, the bird would run (not fly) to claim the kill. This hawk then mantled over the kill and threatened other hawks that approached. Once a hawk had claimed a kill, it was reluctant to fly (I often approached within 3 m of a feeding hawk), and I had to chase it away to recover the specimen. As I drove to different parts of the prairie dog colony, 3 of the hawks followed my vehicle attempting to claim each kill in their vicinity. The 2 others joined approximately 20 White-necked Ravens

(*Corvus cryptoleucus*) in scavenging remains of previously shot prairie dogs. The owner of the land, Homer Ricketson, said that the prairie dog town is hunted for sport frequently, and the hawks appear regularly when shooting begins. Apparently, the hawks have associated the gunfire with an easily obtained food source, since previous hunters have left the prairie dogs.

I would like to thank Gary D. Schnell for reviewing this manuscript.—RONALD K. CHESSER, *Dept. of Zoology, Univ. of Oklahoma, Norman, Oklahoma 73019.* *Accepted 1 Mar. 1978.*

Wilson Bull., 91(2), 1979, p. 331

Misidentified "Eskimo Curlews."—In his admirable "Birds of the Labrador Peninsula and Adjacent Areas" (Univ. Toronto Press, 1963:308), Todd mentions the last specimen of the Eskimo Curlew (*Numenius borealis*) known to have been taken in Labrador. This bird, collected by Ernest Doane on 29 August 1932, at Battle Harbour, was reported by Van Tyne (Wilson Bull. 60:241, 1948). Todd goes on to say that "the same collector had also taken specimens at Red Bay, on September 5, 1926 (one) and August 29 and 31, 1927 (four). These are in the collection of the University of Michigan Museum of Zoology." All 6 specimens are indeed in the collections of this Museum, but only the first is an Eskimo Curlew. The others are Whimbrels (*Numenius phaeopus hudsonicus*) and were catalogued as such by Van Tyne after they were purchased from Walter Koelz in 1929. There is no indication on the labels that they were ever identified incorrectly. I am at a loss to see how this error came about and feel that it should be corrected.

Todd (loc. cit.) deplored the "woefully small" number of specimens of the Eskimo Curlew from Labrador still preserved in scientific collections. While this number is smaller than he believed, it should be pointed out that the critical shortage is in anatomical material of this species. Joseph G. Strauch, Jr., in a search for skeletons of this species was able to find only partial skeletons at the Museum of Comparative Zoology and the United States National Museum. The complete skeleton listed by Ames and Stickney (Postilla 118:17, 1968) as at the Peabody Museum of Natural History, Yale University, is another misidentified Whimbrel. Should remains of Eskimo Curlews be found in the future, it is essential that they be preserved whole in fluid or as skeletons.—ROBERT W. STORER, *Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109.* *Accepted 1 Apr. 1978.*

Wilson Bull., 91(2), 1979, pp. 331–335

The role of parent and helper Red-cockaded Woodpeckers at the nest.—Breeding pairs of Red-cockaded Woodpeckers (*Picoides borealis*) are often assisted by helpers (Baker, pp. 44–59 *in* The Ecology and Management of the Red-cockaded Woodpecker [R. L. Thompson, ed.], Bur. Sport Fish. Wildl. and Tall Timbers Res. Stn., Tallahassee, 1971; Beckett, pp. 87–95 *in* op. cit.; Lay et al., pp. 74–77 *in* op. cit.; Ligon, pp. 3043 *in* op. cit.; and Ligon, Auk 87:255–278, 1970). Information in scanty, however, regarding the relative contributions made by helpers and the mated pair toward incubation and rearing of young. Baker (1971) reported on 2 days of observations of 2 clans that were feeding nestlings. One clan consisted of a mated pair, while the other clan had a mated pair plus 2 male helpers. In the clan of only a pair, both the male and female fed nestlings, with the male being the more active feeder. In the clan of a pair plus helpers, the breeding female was not observed feeding nestlings, and each of the helpers fed more than the breeding male.

The only other quantitative data have been reported by Ligon (1970). At 3 nests attended by only a pair, the males and females participated equally in the feeding of young. At a fourth nest the male made twice as many trips as the female. At 2 nests with helpers, Ligon did not find helpers incubating, but from limited observation he felt that helpers and parents contributed equally to the feeding and brooding of nestlings, to nest sanitation, and to nest defense. Beckett (1971) reported that all clans he studied (number of clans not reported) contained at least 3 adults during the breeding season, but in only 1 clan did helpers assist in rearing the brood. Lay et al. (1971) are the only observers who have reported that birds other than the mated pair incubate.

A certain amount of variability in woodpecker behavior should be expected, not only among clans but also within clans during different periods of the breeding and nesting season. However, the limited information available on the roles played by Red-cockaded Woodpecker breeders and helpers is in some instances contradictory. Over the past 2 years we have accumulated approximately 495 h of observations on 8 clans of Red-cockaded Woodpeckers while they were attending their nests. The data gained on incubation, feeding of the young, and nest sanitation should help clarify the roles of breeders and helpers.

Between 4 May and 30 June 1976, 4 clans of Red-cockaded Woodpeckers, 2 with helpers and 2 without, were observed for 226 h throughout the period during which they were feeding nestlings. Observations were spaced from the 4th or 5th day after the first egg hatched through the age of 22–26 days. Observations were normally conducted between 08:00 and 17:00, but on some occasions we began observations as early as 06:30 and continued until the clan roosted at approximately 19:50. Individual observation periods for a clan ranged from 6 to 13 h in a single day. With 1 of the clans, we conducted only occasional observations. Observations on this clan were normally made between 16:00 and 19:30, and individual sessions ranged from 2 to 3 h. We observed this clan's activities on 8 different days from 7 days after the first chick hatched through the age of 22 days.

In 1977 we monitored incubation as well as the feeding of nestlings. One clan, a pair, was watched from the day the first egg was laid through 11 days after completion of the clutch: 78 h of observation on 13 successive days. In order to determine the onset of incubation, this nest was at first watched from the time the birds left their roosts in the morning until they roosted in the evening. After the birds began attending the nest at extended, regular intervals, observations were conducted for 6–8 h at a time on alternate mornings and afternoons. A second clan, a pair plus a helper, was watched for 43.5 h during 9 successive days from the day the first egg was laid. This second nest was observed for half-day periods (3–6 h), alternating mornings and afternoons, during the entire incubation period. We continued to monitor the activities of the second clan throughout the period of nestling development. We also observed 3 additional clans (2 with helpers, 1 a pair) throughout the nestling period. Observations were scheduled more rigorously in 1977 than in 1976. One clan was observed on 8 days during the nestling period and the other 3 clans on 10 days each. Observations were scheduled to sample activity throughout the period of nestling development. Observation time per clan ranged from 34 to 40 h for a total of 148 h. All observations were conducted between 07:30 and 12:30.

All observations were conducted at the clans' nest trees. Individuals in each clan had been uniquely marked with a series of colored plastic bands so that sex and age (1-year-old or older than a year) were known. No clans contained more than 1 female during the nesting season, and the breeding male was identified by noting which bird roosted in the nest cavity. All other birds attending the nest were considered helpers. Observers were equipped with 30–40× spotting scopes; each time a bird visited the nest they recorded the time the bird arrived, its identity, whether or not it brought food, and the time it left.

Age and sex of helpers.—Red-cockaded Woodpecker helpers are generally believed to be male offspring from previous years (Baker 1971 and Ligon 1970, 1971). Ligon (1970), however, noted 1 female helper in 1 clan, and Baker (1971) noted 2 helpers in 1 clan assisting the breeding pair for 2 successive years. In 1977, 3 of the 4 clans we studied most intensively had helpers. The 4 helpers (2, 1, and 1 per clan) were all males, 2 being offspring from the previous year, and 2 being helpers from the previous year. The age and family lineage of the 2 older birds is not known with certainty since our banding began just prior to the nesting season in 1976. In addition to the 4 clans studied intensively, we collected selected reproduction data on 14 other clans. Six of the 14 clans had helpers, and all 7 helpers were males. Approximate age was known for only 4, 3 being birds that had helped the previous year, and 1 being the offspring of the previous year.

Incubation.—Ligon (1970) had no evidence that helpers incubated. Lay et al. (1971), however, noted 2 males incubating at several nests. While our data on incubation are limited, they clearly show that helpers assisted with incubation (Table 1). Whether or not this holds true in all clans with helpers we do not know. At 1 other nest, however, we observed a helper male spend an hour in a nest cavity which contained 4 eggs. J. A. Jackson (pers. comm.) has also observed helpers incubating in colonies in Mississippi. In both clans the breeding males contributed more time to incubation than did the females. In addition to diurnal incubation, breeding males roosted at night in the nest cavity.

Feeding of nestlings.—In all clans every individual participated to some degree in feeding nestlings. In clans with and without helpers breeding males tended to feed the nestlings more than did the females (Table 2). At 4 of the 8 nests breeding males fed more than females, at 3 nests males and females contributed equally, and at 1 nest the female fed more than her mate. In clans with helpers, the helpers made a major contribution to the total feeding effort (Table 2). The contribution of individual helpers varied, and some helpers contributed as much as or more than did individual breeders. Cumulatively, helpers seemed to participate in the feeding effort in proportion to their numbers.

Brooding and nest sanitation.—In the early stages of nestling development the normal pattern of activity was for the bird bringing food to the nestlings to remain in the nest cavity until another bird arrived with food. All birds bringing food to the nest brooded the nestlings, and there were no major deviations in the brooding pattern from the feeding pattern (Table 2).

The removal of fecal sacs from the nest cavity appears to be a task performed primarily by breeding males. During the 2 nesting seasons reported in this study, we

TABLE 1

CONTRIBUTIONS TO INCUBATION IN 2 CLANS OF RED-COCKADED WOODPECKERS BY PARENT MALES (PM), PARENT FEMALES (PF), AND HELPER MALES (HM)

	Clan 03[1]		Clan 17[2]		
	PM	PF	PM	PF	HM
Mean attentive period (min)	10.9	14.5	28.6	18.7	24.7
Percent of total attentiveness	58%[3]	42%	36%[4]	22%	42%

[1] Total observation time = 4684 min.
[2] Total observation time = 2617 min.
[3] Total attentiveness = 3142 min.
[4] Total attentiveness = 2326 min.

have observed fecal sacs being carried from the nest on 187 occasions. Breeding males accounted for 90% of the observations, breeding females 8%, and helper males 2%.

Reproductive success.—Although Red-cockaded Woodpecker helpers clearly play an active role in incubation and the feeding of nestlings, their effect on reproductive success is still uncertain. Ligon (1970) noted that at 2 nests with helpers, 2.0 young were fledged per nest; whereas, at 7 nests without helpers, 1.4 young per nest were fledged. He suggested that the growth of nestlings might be accelerated by the pres-

TABLE 2

PARTICIPATION IN FEEDING OF NESTLING RED-COCKADED WOODPECKERS BY PARENT MALES (PM), PARENT FEMALES (PF), AND HELPER MALES (HM)

		Percentage contributions of total visits					
Seasonal nestings	Total feeding visits	PM	PF	HM	HM	HM	Cumulative contribution of helpers
Pairs							
08–76[1]	735	67%	33%				
16A–76	513	50%	50%				
08–77	211	55%	45%				
Total and means (%)	1459	59%	41%				
Pairs with helpers							
05–76	196	33%	33%	34%			34%
16B–76	798	27%	27%	23%	13%	10%	46%
11–77	411	26%	30%	27%	17%		44%
16A–77	335	42%	27%	31%			31%
17–77	283	29%	23%	48%			48%
Total and means (%)	2023	30%	27%				42%

[1] Seasonal nestings are identified by clan number (08) followed by the calendar year ('76) of the nesting season.

TABLE 3

NUMBER OF YOUNG FLEDGED BY RED-COCKADED WOODPECKERS DURING 2 BREEDING SEASONS FOR PAIRS WITH AND WITHOUT HELPERS

	Number of pairs		Fledglings per pair (mean)		Fledglings per pair (range)	
Year	Without helpers	With helpers	Without helpers	With helpers	Without helpers	With helpers
1976	3	5	1.3	1.6	0–2	0–4
1977	8	8	1.9	2.4	1–3	1–3

ence of helpers, but his sample size was too small for a conclusive comparison. Our data on the effects of helpers on reproductive success are also still inconclusive.

Over the 2 breeding seasons reported in this study, 1976 and 1977, we have collected data on clutch-size, hatching success, and fledging success from a total of 24 nestings involving clans of known size. Eleven of the nestings were by breeding pairs and 13 were by pairs plus helpers. In both years, clans with helpers had an average fledging success higher than pairs alone (Table 3). Reproductive success, however, is affected by factors other than the mere presence of helpers, such as interspecific competition for cavities, nest depredation, habitat quality, and possibly intraspecific social interactions. Until we can better assess the effects some of these additional factors have on reproductive success, and determine possible interrelationships between selected factors such as clan size and habitat quality, we do not feel the effect of helpers on reproductive success can be clearly distinguished from other possible influences.—MICHAEL R. LENNARTZ AND RICHARD F. HARLOW, *U.S. Dept. of Agriculture, Forest Service, Southeastern Forest Experiment Station-Dept. of Forestry, Clemson Univ., Clemson, South Carolina 29631. Accepted 18 May 1978.*

Wilson Bull., 91(2), 1979, pp. 335–338

Three-week vs 4-week nestling periods in *Picoides* and other woodpeckers.—A striking fact about the nesting of Downy Woodpeckers (*Picoides pubescens*) is that their nestling period is of 3 (Lawrence, Ornithol. Monogr. 5:1–156, 1967) instead of 4 weeks (or thereabouts) as it is for the 4 other woodpeckers with which they are sympatric, namely the Hairy (*P. villosus*) (Lawrence, op. cit.) and Pileated (*Dryocopus pileatus*) (Hoyt, Auk 61:376–384, 1944) woodpeckers, the Common Flicker (Sherman, Wilson Bull. 22:135–171, 1910) and the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Kilham, Wilson Bull. 89:310–324, 1977a). Why should this be?

One might say it is a matter of the downy being able to develop faster because it is of smaller size. That this is unlikely is shown by data given for 4 central European species also of the genus *Picoides* (Table 1). Of these 3, the Lesser (*P. minor*), the Middle (*P. media*) and the Greater (*P. major*) Spotted woodpeckers all have, like the downy, a 3-week nestling period, although *P. major* is of the same approximate size as *P. villosus*. Furthermore if size made a difference, why should the Pileated Woodpecker and its

TABLE 1

EIGHT SPECIES OF WOODPECKERS USED TO ILLUSTRATE THE HYPOTHESIS THAT THOSE WITH A 3-WEEK NESTLING PERIOD NEST IN DEAD AND DECAYING TREES (RELATIVELY UNSAFE) WHILE THOSE WITH A 4-WEEK NESTLING PERIOD NEST IN TREES WITH TOUGHER WOOD THAT OFFER BETTER PROTECTION (FOR COMPLETE DISCUSSION SEE TEXT).

	Species	Length nestling period (days)	Body length[1] (cm)	Type of nest tree preferred	Source
American	*Picoides pubescens*	19–22	16.5–17.8	Dead, decayed	Lawrence 1967 Kilham (ms) Hadow 1976
	P. borealis	26–29	21.7	Living (with heart rot)	Ligon 1970[2]
	P. villosus	28–30	21.7–26.7		Lawrence 1967, Kilham 1968
	Sphyrapicus varius	26–28	20.4–21.6		Lawrence 1967 Kilham 1971, 1977a
European	*P. minor*	18–21	14.7	Dead, decayed	Westerfrölke 1955[3] Witherby et al. 1943[4]
	P. medius	22	21.7		Steinfatt 1940[5]
	P. major	21–22	23		Pynnönen 1939
	P. leucotos	27–28	25.5	Living (or dead)	Pynnönen 1939 Ruge and Weber 1974

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[1] Taken from Peterson (A Field Guide to the Birds, Houghton Mifflin Co., Boston, 1947) and Peterson et al. (A Field Guide to the birds of Britain and Europe, Houghton Mifflin Co., Boston, 1954).

[2] Auk 87:255–278, 1970.

[3] Vogelwelt 76:185, 1955.

[4] The Handbook of British Birds, H. F. and G. Witherby Ltd., London, 1973.

[5] Beita zur Fortflanzungbiol. der Vogel 16:93–99, 1940.

European counterpart, the Black Woodpecker (*D. martius*) (Pynnönen, Ann. Soc. Zool. Bot. Fennica Vanamo 7:1–166, 1939), have the same 4-week nestling period as the smaller hairy or the sapsucker?

Before discussing the length of nesting periods in terms of selection, Hadow's ideas (North Am. Bird Bander 1:155–164, 1976), expressed in relation to Lack (Ecological Adaptations for Breeding in Birds. Methuen and Co., London, 1968), on the longer nestling periods of woodpeckers as compared to those of passerines with open nests are worth repeating. What Hadow states is that "since nest holes are relatively safe from predation there is little selection pressure to get away from the nest early" and, second, that the longer period allows nestlings to become more mature and hence better able to look after themselves at time of fledging.

A key point I would make is that although nest holes are relatively safe from predators, some types are more safe than others. Woodpeckers with stronger bills can build nests in living trees that have heart rot due to fungal action at the center. Species building nests of this type are the Red-cockaded (*P. borealis*) (Steirly, Atl. Natur. 12:280–292, 1957) and Hairy (Kilham, Wilson Bull. 80:286–305, 1968) woodpeckers as well as the Yellow-bellied Sapsucker (Kilham, Wilson Bull. 83:159–171, 1971) and the White-backed (*P. leucotos*) Woodpecker (Pynnönen, op. cit.). All of these species have 4-week nestling periods (Table 1).

Seemingly less secure nests, in terms of wind damage or of predators chewing their way in, are those built in dead, decaying wood by species with weaker bills. These, as shown in Table 1, all have 3-week nestling periods.

An objection is that Hairy Woodpeckers and sapsuckers sometimes nest in dead, decaying stubs. But from years of watching both species (Kilham 1968, 1971 and 1977a) I believe that they do this not by choice but by necessity. Lawrence (op. cit.) also notes that the hairy prefers to nest in living trees. As far as the White-backed Woodpecker of Europe goes, I hazard a guess that the same situation holds, for Ruge and Weber (Vogelwelt 95:138–147, 1974) point out that this species has the strongest bill of all the native *Dendrocopos* (*Picoides*) species. While they describe it as nesting in dead trees in the Alps, Pynnönen (op. cit.) describes 2 of 4 pairs as nesting in living trees in Finland.

Although species of all sizes use dead trees affected by heart rots (Connor, Miller and Adkisson, Wilson Bull. 88:575–581, 1976) the downy, in the experience of Connor et al. (1975) still selected trees that were softer, i.e., more rotted than those used by the hairy and pileated. The important factor is the actual hardness of the wood. Expressed in this way, woodpeckers with strong bills can build more secure nests, whether in living trees or dead ones that are still comparatively hard.

A further point is that a small woodpecker with a relatively weak bill will be less able to defend its nest holes against predators. As described elsewhere (Kilham 1968), a hairy, even though nesting in a well decayed birch stub, was able to defend its nest against a raccoon (*Procyon lotor*). It seems doubtful if a downy could have survived under similar circumstances.

A difficulty in discussing evolutionary problems concerning woodpeckers is that the virgin forests in which their evolution took place have been replaced with the woods of different composition in which we study them today. In spite of these difficulties, I feel that the 3-week vs the 4-week nestling period is a problem worthy of study. I have arbitrarily selected only a few species to discuss, mostly on the basis of their being in the genus *Picoides*. Other genera with other adaptations meet problems in other ways. Red-headed Woodpeckers nest in dead stubs (Kilham, Wilson Bull. 89:164–165, 1977b) in open situations, but they are aggressive birds and hence able to survive in situations where hairies and downies might not.

Acknowledgments.—I would like to thank Richard N. Connor and Harlo H. Hadow for helpful comments and criticisms.—LAWRENCE KILHAM, *Department of Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755.* *Accepted 24 June 1978.*

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Breeding activities of Waved Woodpeckers in Surinam.—Species of the essentially neotropical woodpecker genus *Celeus* range from Mexico to northern Argentina (there is 1 Asian representative, *Celeus brachyurus*). Due to generally sparse distribution, shyness, and relatively non-vocal habits, and for some species, a deep forest habitat, this group is 1 of the least known of neotropical picid genera. Nests are known for the Pale-crested Woodpeckers (*C. lugubris*) (Short, Amer. Mus. Novitates 2413:1–37, 1970; Short, Bull. Amer. Mus. Nat. Hist., 152:253–364, 1973b) and the Chestnut Woodpecker (*C. elegans*) (ffrench, A Field Guide to the Birds of Trinidad and Tobago, Livingston Press, Wynnewood, 1970:270); for these and all other species only casual observations of biology and behavior have been published.

I studied Waved Woodpeckers (*C. undatus*) from 20 March to 15 May 1977 at the Raleigh Falls Nature Reserve, a 56,000 ha area on the Coppename River about 100 km south of its termination on the Atlantic coast of Surinam. Most observations were made on the southernmost tip of Foengoe Island, a small island within the reserve mostly covered with "high river bank forest" and partially cleared for houses and a grassy airstrip. The canopy layer of the forest was typified by a *Mouriri* sp., with emergents *Jacaranda copaia*, *Inga alba*, and *Ceiba petandra*, and understory dominated by the spiny palm *Astrocargum sciophilum*. Second growth of the disturbed areas around the forest edges was dominated by *Cecropia surinamensis* and *C. sciadophyllus*.

Surinam's climate is tropical, and heavy rains begin between mid-April and mid-May and extend to August. Hatching of the young I studied seemed to have been synchronous with the onset of the rainy season.

I made observations at a Waved Woodpecker nest for 4–6 h a day for 47 days from about 20 m away, using 7 × 35 binoculars. Sightings of Waved Woodpeckers in the forest were otherwise rare because of their tendency to forage high in the dense forest canopy.

Vocalizations.—The 1 vocalization heard continually from the Waved Woodpeckers was a very distinctive disyllabic call: a rising, liquid note followed by a descending, more guttural one, the entire call approximately 1.25 sec in duration. The physical process involved in vocalizing could be seen as each of the woodpeckers leaned out of the nest hole to call its mate. The first part of the call was accompanied by a lurching forward and raising of the crest, and the second syllable brought a relaxation of this swelling movement. Another vocalization, heard but once, was a chattering given in alarm during a brief encounter with a woodcreeper (*Dendrocolaptes* sp.).

Although both male and female Waved Woodpeckers reportedly drum (Haverschmidt, Birds of Surinam, Livingston Press, Wynnewood, 1968), the difficulty in sighting them prevented observation of their drumming. From time to time I heard drumming which may have been of this species in the vicinity of the nest excavations.

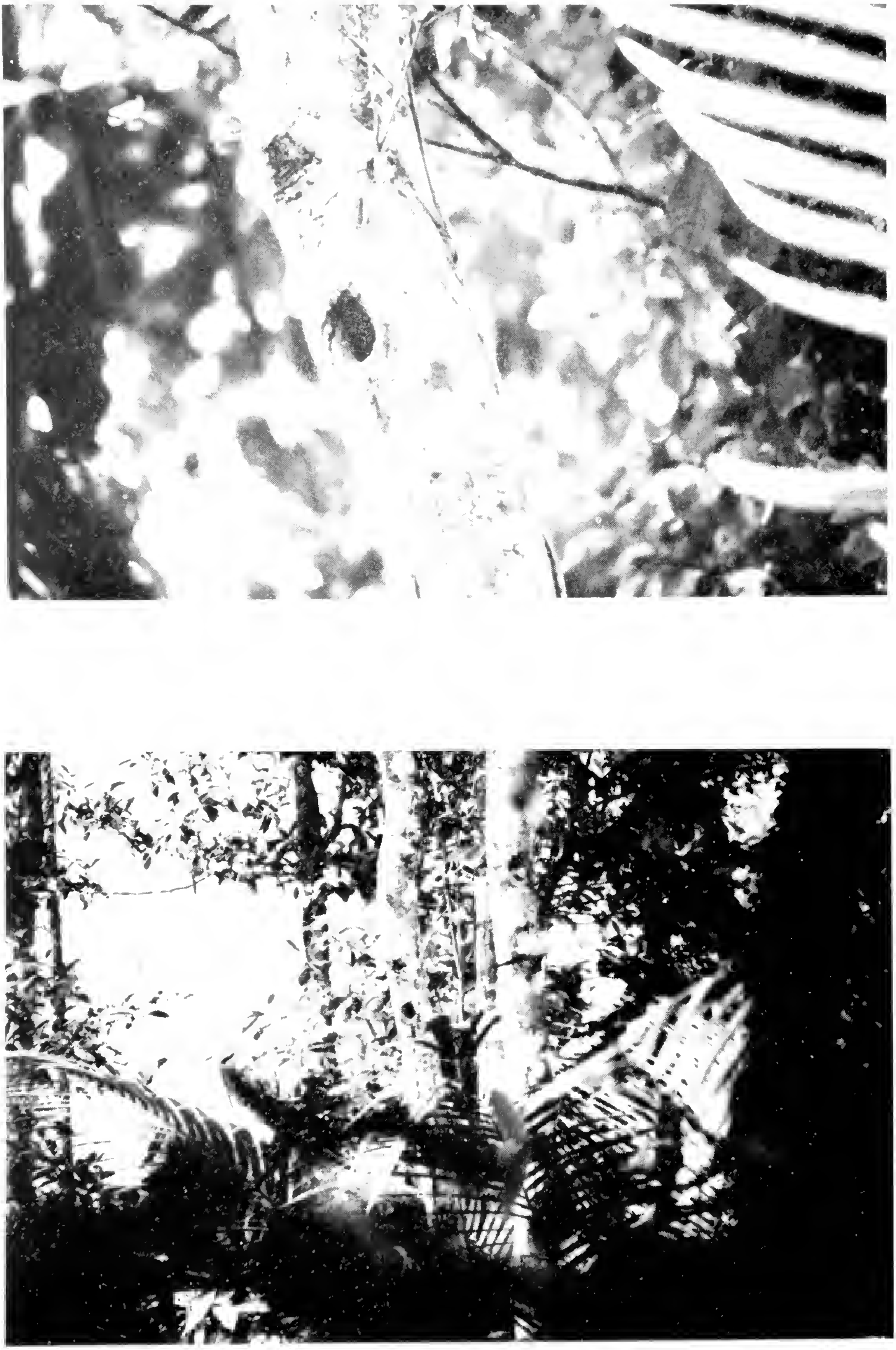

FIG. 1. Above, nest; below, nest-site of a pair of Waved Woodpeckers.

TABLE 1

NEST ATTENDANCE BY MALE AND FEMALE WAVED WOODPECKERS

Minutes spent excavating or guarding the hole			
Date	Observation period	Male	Female
28 March	225	110	50
29 March	225	140	40
30 March	280	125	50
31 March	240	30	0
2 April	240	180	50
(Totals)	1210	585 (48.34%)	190 (15.70%)

Minutes spent incubating during daylight hours						
	06:00–10:00		10:00–14:00		14:00–18:00	
Dates	Male	Female	Male	Female	Male	Female
6–8 April	120	120	0	240	130	140
9–11 April	20	190	0	240	190	70
12–14 April	60	170	0	200	120	90
(Totals)	200	480	0	680	440	300

Male total*: 640 (29.62%) Female total: 1460 (67.59%)

*The male also spent from 18:30 to 06:00 in the hole each night.

Frequency at which nestlings were fed						
	06:00–10:00		10:00–14:00		14:00–18:30	
Dates	Male	Female	Male	Female	Male	Female
23, 24, 22 April	1	1	1	1	3	2
25, 27, 28 April	2	1	1	1	0	1
29 April; 2, 3 May	1	1	1	1	0	2
(Totals)	4	3	3	3	3	5

Male total: 10 Female total: 11

Nest excavation and defense.—On 26 March the sound of persistent pecking led me to the excavation of these Waved Woodpeckers. The hole was about 5 m up in a live *Guarea kunthiana* which was about 18 cm in diameter at the level of the excavation (see Fig. 1). The nest cavity was already large enough for either pair member to sit inside of it while working on the inner walls. During the next week, the male Waved Woodpecker spent more time at the hole than the female during the morning, when all observation took place (Table 1).

From 27 March to 3 April, the pair spent progressively less time excavating, and the attendant bird spent more time sitting quietly inside the hole. At first it perched on the inner rim and looked out of the entrance, and by 1 and 2 April, long periods of time passed as each pair member perched inside the excavation, appearing at the hole entrance every 1 or 2 h. I could occasionally still hear sounds of excavating from the cavity.

I checked the nearly finished excavation at dusk on 26 and 27 March to determine at what point 1 of the pair would begin roosting overnight in the hole. A male Guianan Toucanet (*Selenidira culik*) used the excavation as a roost. He arrived to roost at 18:35 each of the 2 evenings, perched momentarily on the rim of the hole, and poked his bill and head in several times before popping in head first. After entering, he looked out of the hole for a few min before retreating further down, presumably for the rest of the night.

On 30 March, the male Waved Woodpecker spent the night in the hole for the first time. He entered at 18:00 and was there when the toucanet came in at 18:15. Over the next 10 min the toucanet put his head down into the hole again and again, sometimes leaning into it up to his wing coverts, and delivering repeated jabs toward the woodpecker inside. A few squawks came from the male woodpecker. Within 6 min the toucanet left and another male toucanet (I could see the first perching about 20 m away) approached the hole—and after poking into it several times actually entered the excavation. I heard scuffling and squawking and the toucanet emerged in ca. 1 min to fly off again. The other 1 then returned to the hole and was putting his head inside again when I approached and clapped my hands. The 2 intruders flew toward the nearby clearing, and by 18:30 neither had returned. Meanwhile the woodpecker had stuck his head out of the hole, his bill slightly open as though panting, before retreating for the night. He then continued using the nest as his nightly roost through the duration of my study.

Thus it appears that these woodpeckers are in competition with the toucanets for excavations. Similar instances of competition between woodpeckers and ramphastids have been described, for example, between Pale-billed Woodpeckers (*Campephilus guatamalensis*) and Collared Aracaris (*Pteroglossus torquatus*) in Guatamala (Kilham, Auk 94:774–775, 1977), and between Crimson-crested Woodpeckers (*C. melanoleucos*) and Collared Aracaris in Panama (Kilham, Wilson Bull., 84:28–47, 1972). I also have seen crimson-cresteds harrassed and displaced from roost holes by Chestnut-eared Aracaris (*P. castanotis*) in eastern Peru.

Courtship and communication during nest excavation.—There seemed to be a close bond between the members of the Waved Woodpecker pair. This was characterized not only by cooperation in nest-building and in the sharing of parental duties, but also by frequent vocal exchanges as the woodpeckers alternately excavated and guarded the hole. After a period of 1 or 2 h in the hole, the occupant leaned out and called; the mate most often answered immediately and/or flew in to perch on the outer rim of the hole. If the mate did not appear in a few min, the bird in the hole continued to call up to 25 or 30 times, and then eventually flew from the hole.

When the mate did arrive, it usually looked into the nest several times then waited, perched outside, until the bird inside emerged and left; the arriving bird then slipped in head first. Several times, however, the bird inside appeared reluctant to leave, and both ended up in the hole at once. The pair would then appear at the entrance, sometimes taking turns at looking out, and sometimes squeezing to peer out together. Once both birds were inside the hole for 40 min; part of the time the male excavated on the bottom while the female looked out.

FIG. 2. Tapping upon the inner rim of the nest hole by the female Waved Woodpecker as the male is perched outside.

It was also at the time of changing places at the nest hole that I observed 1 form of courtship display. As the male flew in to land on the rim, the female began tapping rapidly and softly at the inside rim, a gesture identical to the demonstration tapping (termed "Drum-tapping" by Kilham [Condor 61:337–387, 1959]) described for several species of woodpeckers (Blume, Vogelring 27:65–74, 1958; Kilham, op. cit.; Kilham, Wilson Bull. 84:28–47, 1972). I did not see the male tapping in this manner (see Fig. 2).

On 29 March it appeared that copulation nearly took place before a woodcreeper disrupted the pair. At 07:15 I heard 2 Waved Woodpeckers calling back and forth to each other near the nest hole. The male soon landed on the outer rim of the hole, continuing to exchange vocalizations with a second woodpecker nearby. After 2 min and 7 vocal exchanges, the male flew toward the other. I located the pair less than a min later about 12 m up in a partially dead tree. Here they exchanged calls in rapid succession, the female compressing herself horizontally while perching on and perpendicular to a thin branch, the male approaching slowly from below her. These postures are similar to those I have seen in other woodpecker species (Pileated Woodpecker [*Dryocopus pileatus*], Lineated Woodpecker [*D. lineatus*], and *Campephilus melanoleucos*) immediately preceding coition. Suddenly, however, a woodcreeper (species?) flew at the male and the 2 woodpeckers chattered as they excitedly flew away. Within 40 min the female had returned to the hole, and for the rest of the morning the pair alternated at guarding it as usual.

During each of the next 3 days the pair spent several morning hours away from the nest while their vocal exchanges and what I judged to be their drumming could be heard in the treetops nearby. Because of the apparent copulation attempt and the timing of breeding activities, I imagine that the matings were then taking place away from the nest excavation.

Incubation.—I presume eggs were laid around 3 April, as this was the first day that no excavation whatsoever was heard, and the male sat quietly out of sight for the entire 4½ h of observation. From this day on, the woodpecker pair vocalized rarely, changed places at the nest quickly and silently, and each spent longer periods than before at a time—up to 4 h or more—out of sight in the hole.

Starting 6 April, observations were systematized so that all daylight hours were covered over a period of 3 days. The following pattern emerged (see Table 1): the male spent the night in the hole, and remained there for several hours after daylight, when the female replaced him. She usually spent through midday and early afternoon in the hole. They changed places again for shorter periods in the late afternoon, with the female taking the last shift before the male came in to roost for the night, between 17:30 and 18:30.

Nestlings.—I left the nature reserve on 15 April and returned on 23 April. By this time the woodpeckers were feeding nestlings, of which subsequent observations suggested there were 2. The feeding duties were shared by the parents throughout the day (Table 1). They apparently fed the young by regurgitation as I never saw live prey in the bill of a parent. Skutch (Auk 65:225–260, 1948) noted that such long intervals at which the young are fed are indicative of regurgitative feeding. The male and female alternated in their visits and usually the feeding parent left with a fecal sac in its bill.

On 25 April an aboreal snake entered the nest hole by approaching along the trunk above. A faint chattering could be heard while the snake was in the hole. It emerged 3 min later, coming out little by little over a period of 8 min, its middle swollen from its swallowed prey. Once starting down the tree trunk, it left quickly.

By 26 April, the remaining nestling's chattering was loud enough to be heard plainly from my observation spot. The 1 young began calling as soon as the parent bird landed on the tree. After the parent entered the hole there was silence for about 15 sec, doubtless as food was transferred, then chattering began again and continued for up to 3 min after the parent left. The parents continued to feed the remaining nestling until

3 May when again the same species of snake entered the hole and swallowed the small woodpecker. I had not seen the snake entering the hole but caught it after it had left the nest. The snake was collected and the nestling and snake preserved.

Charles Myers of the American Museum of Natural History identified the snake as *Pseustes poecilonotus polylepsis* (AMNH 115650, Herpetology). The nestling (AMNH 7633, Ornithology), examined by Lester Short of the same institution, was about 12 days of age, had the eyes opened, and the egg tooth essentially gone. Well developed "heel" pads were evident. Feathers of the capital tract were moderately developed; the dorsal tract was but slightly feathered except on the upper back before dividing into lateral extensions that met above the uropygial gland; the ventral tract was well developed as was the femoral tract; and the crural tract was but slightly developed. Tail feathers coming in and out of the sheaths were the rectrices and a row of coverts above and below them. Wing feathers well developed and considerably out of the sheaths were the remiges, the greater coverts, some of the next row of coverts, the alular feathers, the feathers along the front of the wings, and the humeral feathers. Primary 1, but not primary 2 was much abbreviated (for discussion of abbreviated inner primaries of woodpeckers see Chapin [Auk 38:531–552, 1921] and Sibley [Auk 74:102–103, 1957]); the first primary was but ⅓ the length of the other primaries, including the sheath, the projecting feather out of the sheath was but ⅕ the length of the other primary feathers emerged from their sheaths, and in length and its small diameter, the first primary was the size of smaller greater covert feathers.

Interaction with other species.—Apart from the instance described earlier, I saw the Guianan Toucanets at the hole twice more during the study period. On 11 April the 2 males came to the hole at 13:50 while the female Waved Woodpecker was incubating. One toucanet perched at the rim and poked his head in several times before I chased them away. At 15:00 on 26 April, while there was a single nestling in the hole, a toucanet came to perch and probe into the hole; again I chased him away.

Other interspecific interactions not previously mentioned included 2 instances when a Chestnut Woodpecker (*Celeus elegans*) landed on the nest tree and approached the hole (it left within 7 sec), after which the Waved Woodpecker inside merely appeared at the entrance momentarily before retreating back into the hole. After the second nestling was taken by the snake, the parent woodpeckers were not seen at the hole again. Neither they nor the toucanets roosted in the hole thereafter.

Acknowledgments.—This study was supported by a 1976 Thomas J. Watson Fellowship. I am indebted to Lester L. Short for his suggestions regarding the study, as well as for his description of the nestling woodpecker and comments upon the manuscript, to Lawrence Kilham for his suggestions regarding revisions, and to Charles Myers for his identification of the snake. I also thank J. P. Schulz and Henri Reichart, of the STINASU division of the Surinam forestry service, for their assistance while I was in Surinam. Fritz von Troon of STINASU and Marc G. von Roosmalen aided in identification of trees and in forest type description. Finally, I thank Paul K. Donahue for assistance with the woodpecker drawing and for his suggestions on the manuscript.—PATRICIA O'BRIEN, *Department of Psychology, University of Connecticut, Storrs, Connecticut 06268.* *Accepted 19 June 1978.*

Wilson Bull., 91(2), 1979, pp. 345–346

Drowning of grassland birds in stock tanks.—Drownings of birds in man-made structures are probably common occurrences, although there are few reports of large numbers of drowned birds. Known examples of birds drowned in stock tanks (Craig and Powers, Condor 78:412, 1976; Enderson, Auk 81:339, 1964) or in impoundments (Mullan and Applegate, Wilson Bull. 81:467, 1969) include American Kestrels (*Falco sparverius*), a Prairie Falcon (*Falco mexicanus*) and Bobwhites (*Colinus virginianus*).

I report here the finding of at least 25 drowned Lark Buntings (*Calamospiza melanocorys*) and 113 Western Meadowlarks (*Sturnella neglecta*) in 2 adjacent watering tanks in southeastern Montana (Rosebud County, Range 43E, Township 1N). Both species are common summer residents in this area of the northern Great Plains. On 1 September 1976, I looked into these roadside tanks and counted nearly 50 dead birds. Neither tank had been used for livestock watering during the previous 5 months. The largest tank (6.6 m diam.) contained 43 carcasses floating in about 10 cm of water, while the smaller tank (2.6 m diam.) contained 6 carcasses in 6 cm of water. In each tank a dense algal bloom was suspended in the water. Vegetation near the tanks included sagebrush (*Artemesia* spp.), post-bloom yellow sweetclover (*Melilotus officinalis*), lamb's quarters (*Chenopodium album*) and several species of dry prairie grasses.

On 27 May 1977, I returned to the tanks and collected 138 bird skulls from the large tank only. Of these skulls 113 belonged to the Western Meadowlark and 25 to the Lark Bunting. By examing the extent of ossification in each skull, I established 2 age groups of both species and found that 23 bunting and 77 meadowlark skulls were only partially ossified. These were probably birds of the year. In support of this, I also noted from plumage characteristics that most carcasses in the tanks were those of young birds, especially the buntings. Accurate age classification of 10 meadowlark skulls could not be made because of damage to or deterioration of them.

The magnitude of these drownings presents an unresolved enigma. Unusually heavy spring and summer rains in 1976 probably kept the tank bottoms covered with some water and replenished throughout the summer. Rain gauge data taken from a site about 8 km away showed that 23.3 cm of rain fell between 15 April and 1 September 1976, but less than half of that in 1977. Hence, neither water nor birds were seen in these tanks in 1977. Because most of the buntings and meadowlarks were young birds, one might speculate that lack of experience near watering troughs was involved, but this seems unlikely since large numbers of juveniles of both species are normally present in the area during late summer. Individual birds may have attempted to drink as well as bathe in the tank, but adherence of the algae to the feathers may have precluded flight from the tank, especially since no algal mats that might serve as launching platforms were present. This problem may have been exacerbated by an intensifying algal bloom probably fed by the end products of animal decomposition. Pathological studies of these birds were not considered because of the extent of decomposition and the remoteness of the site from an appropriate laboratory for examination.

Assuming that both species could detect these stationary water sources aloft despite the algal camouflage, it is possible that a flock of birds descended to the tank and many were subsequently pushed into the water and drowned. Some birds may have even mistaken this algal "broth" for solid ground and consequently drowned after landing directly in the water. On the other hand, it has been suggested to me that these birds may have been sick, subsequently became attracted to the water, and died by falling into the tank. Clearly, further information is necessary to fully evaluate all of these possibilities. Although Craig and Powers (op. cit.) suggested that a block of wood be placed in watering tanks to prevent episodes of drowning, the sizable wood slab I found in the large stock tank ostensibly prevented few avian deaths.—John D. Chilgren, *Department of Zoology, Oregon State Univ.,* and *Corvallis Environmental Research Laboratory, Corvallis, Oregon 97331. (Present address: NCNM, 510 SW 3rd, Portland, Oregon 97204.) Accepted 10 June 1978.*

REQUESTS FOR ASSISTANCE

Shorebird color-marking.—In 1979, the Canadian Wildlife Service will be continuing a large-scale program of banding and color-marking shorebirds in James Bay. Since 1974, over 38,500 shorebirds have been captured, resulting in more than 1700 "bird days" of sightings of dyed birds ranging from eastern Canada to South America. Much valuable information on migration routes and strategies is being obtained and observers are again asked to look out for and report any color-dyed *or* color-banded shorebirds that they may see. Reports should include details of species (with age if possible), place, date, color-marks and, if possible, notes on the numbers of other shorebirds present. For color-dyed birds, please record the color and area of the bird that was dyed. For color bands and standard metal leg bands, please record which leg the bands were on, whether they were above or below the "knee", the colors involved (yellow or light blue), and the relative position of the bands if more than one was on a leg (e.g., right lower leg, blue over metal, etc.). All reports will be acknowledged and should be sent to: Dr. R. I. G. Morrison, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario, Canada K1G 3Z7.

International shorebird surveys 1979.—A cooperative International Shorebird Survey scheme has been organized by the Canadian Wildlife Service and the Manomet Bird Observatory since 1974 to obtain information on shorebird migration and to identify and document areas of major importance. Valuable information has come from contributors throughout eastern Canada and the U.S.A., the Caribbean Islands and Central and South America, and is being used in assessing requirements for the future protection and conservation of the birds and their habitat. We plan to continue the project in 1979. Any observer who may be able to participate in regular counts of shorebirds during spring and autumn migration periods, as well as during the winter in shorebird wintering areas, is asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome. For areas in Canada: Dr. R. I. G. Morrison, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario, Canada K1G 3Z7. For areas in U.S.A., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, Massachusetts 02345.

REQUEST FOR ASSISTANCE

Bird records needed.—Records of birds observed in Western Alaska on the Seward Peninsula, Norton Sound area and St. Lawrence, King, Diomede and Sledge islands, for inclusion in a publication of the avifauna of this area. Full credit will be given. Send reports to: Henrich Springer, Box 352, Nome, Alaska 99762.

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ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in memory of the late Aaron M. Bagg, former president of the Society. The Student Membership Committee has designated the award recipients for 1979 as follows: James C. Bednarz, Iowa State University; James L. Blank, Indiana University; Daniel C. Butler, Colorado State University; Carl D. Cooley, Mississippi State University; Jeffrey A. Cox, University of Florida; Louis C. Farley, Idaho State University; Martha B. Hays, Mississippi State University; Barbara J. Hill, Iowa State University; Ellen J. Johnson, Iowa State University; Michael D. Koob, University of North Dakota; Joan M. Lindeburgh, University of Arkansas; Kenneth D. Meyer, University of North Carolina; Thomas A. Nigus, Iowa State University; Richard D. Rowlands, Indiana University; Seri G. Rudolph, University of California; Barbara Sherman Simpson, University of North Carolina; Maile A. Stemmermann, University of Hawaii; and Mark C. Witmer, Texas A&M University.—JAMES R. KARR, *Chairman, Student Membership Committee.*

NOTICE TO MEMBERS

Effective immediately, Robert D. Burns has become the new Treasurer for The Wilson Ornithological Society, replacing Ernest E. Hoover. Appropriate correspondence should be directed to Dr. Burns (see inside front cover for address). The Wilson Ornithological Society thanks Ernest E. Hoover for his years of fine work for the Society and welcomes Dr. Burns in this capacity.

JOSSELYN VAN TYNE AND ALEXANDER WETMORE MEMORIAL AWARDS

The A.O.U. solicits applications for research grants from these funds. The Van Tyne awards will consider any aspect of avian biology; the Wetmore awards are limited to taxonomy/systematics. Grants are usually in amounts of a few hundred dollars. Preference is given to students and other persons without other sources of funds. Applicants should send 4 copies of the following: (1) a 3–5 page description of research goals and procedures; (2) an itemized budget, with a justification of major items and the total amount requested; and (3) a brief resume of academic/ornithological experience. In addition, all applicants should request 2 or 3 letters of recommendation from recognized ornithologists, to be sent directly by the writers. All application materials, including letters, must be received before 21 June 1979. Send all materials to Dr. A. S. Gaunt, A.O.U. Committee on Research Awards, Department of Zoology, The Ohio State University, 1735 Neil Ave., Columbus, Ohio 43210.

Wilson Bull., 91(2), 1979, pp. 348–365

ORNITHOLOGICAL LITERATURE

THE HERONS OF THE WORLD. By James Hancock and Hugh Elliott. Harper and Row, New York, 1978: 304 pp., 61 color plates, 10 halftone drawings, 4 pages of maps. $65.00.—When I first began to explore the ornithological literature some 40 years ago, the great color-illustrated monographs of the 19th and early 20th centuries held a particular fascination for me, epitomizing a bygone era of opulence. As a child of the Depression years, I wondered what it must have been like to order routinely for one's personal library (always envisioned with a balcony and a fireplace) such works as those of Gould, D. G. Elliott, Sclater, and Sharpe. It never seemed right to learn of a dollar cost for such treasures—somehow it seemed more appropriate that they should be priced in guineas.

The incessant flow of bird books in subsequent years has been mentioned by many authors and reviewers. Most of these books, if illustrated in color, have been regional, either such elaborate and costly works as Bannerman on West Africa, the British Isles, and the Atlantic Islands, or field guides to satisfy the needs of the increasingly peripatetic army of bird watchers.

More recently we have seen a return to the publication of large, relatively expensive monographs of taxonomic groups of birds, started by Delacour's "Pheasants of the world" (1951), and including such works as Brown and Amadon's "Eagles, hawks and falcons of the world" (1969), Delacour and Amadon's "Curassows and related birds" (1973), Forshaw's "Parrots of the world" (1973) and "Birds of paradise and bower birds" (1977), Ripley's "Rails of the world" (1977), and too many books on waterfowl and owls to possibly list. Some family monographs have been somewhat more modest in format and less lavishly illustrated, such as Gilliard's "Birds of paradise and bower birds" (1969), Goodwin's "Pigeons and doves of the world" (1967) and "Crows of the world" (1976).

Taking an honored place among these monographs is the beautifully produced book on herons by James Hancock and Sir Hugh Elliott. Although it has some flaws, as an example of the fine art of the bookmaker (designed by London Editions Ltd., with printing and binding by Amilcare Pizzi of Italy) it is equalled or surpassed only by Ripley's rail monograph and the original edition of Forshaw on parrots, and, at 9½ × 14 × 1¼ in., is a much more manageable size than either of the others.

Although the texts of such books should be their most definitive features, most people who have thumbed through the heron monograph have commented to me on the plates; these tend to be quickly (and often superficially) evaluated by those who have neither the time nor the inclination to *read* the book. In deference to this first-impressions approach, therefore, I will begin with my own commentary on the illustrations. The halftones are all by Robert Gillmor, surely England's (if not the world's) most productive bird artist, and the color plates are by Gillmor and a lesser-known English artist, Peter Hayman. Although Hayman's paintings are not really *bad*, they seem to be responsible for most of the negative reactions to this book that I have heard, though I tend to prefer them to the anatomically impossible grotesqueries in "Rails of the world." Hayman does not yet belong in the league of Gillmor, Gilbert, Eckelberry, Tudor, and other illustrators of recent major works. Many of his paintings are annoyingly stiff, looking as if they had been painted directly from mounted birds: see, for example, the 4 *Botaurus* and the tiger-herons. Hayman also tends to adhere to the school of bird art that believes every feather should be shown; compare his plate of the white *Ardeola idae* with Gillmor's paintings of the various white egrets. The 2 Cattle Egret (*Bubulcus ibis*) figures on Gillmor's plate stand 17 and 13 cm high, and Gillmor understands that if living Cattle Egrets were at a distance from the observer such that their *apparent* size were 17 and 13 cm, the eye would simply not see the margins of each of the white body feathers. Although most of Hayman's figures are no more than profiles of standing birds, a few of his paintings are more lively and successful, such as the series of *Ixobrychus* bitterns flying and at the nest. His most daring attempt, a head-on view of the Boat-billed Heron (*Cochlearius cochlearius*) in display, verges on the disastrous, as he does not understand such matters as the interrelationships of feather tracts and the anatomy of legs. The very broad crest feathers, which number fewer than 2 dozen (see photograph in Rand 1966), are shown as approximately 80 narrowly linear feathers. Fortunately the species account of *Cochlearius* is also illustrated by a small halftone by Gillmor, showing the species in a more relaxed and lifelike pose.

Gillmor's paintings always seem more alive, even if the bird is portrayed in a simple profile and not "doing" anything. Frequently, however, his herons are shown in typical foraging positions. He often uses 2 or more figures on a plate showing characteristic poses such as birds with necks extended and drawn back. In general, I find Gillmor's paintings highly attractive, although in a few instances (presumably species with which he has had little or no field experience), he fails to catch the "jizz" (as the British call the general distinctive overall appearance and attitude); in this category I would place his plates of the Little Blue (*Egretta caerulea*) and Tricolored (= Louisiana) (*E. tricolor*) herons. His foraging Reddish Egret (*E. rufescens*) is properly lively, but not nearly shaggy enough. For a few little-known species, his plates are almost as stiff as those of Hayman, notably the 4 species assigned in this book to the genus *Gorsachius*. In connection with the latter genus, it is a pity that only the adults of *melanolophus* and *leuconotus* were portrayed, as their juvenal plumages are far more different from the adults than are those of the figured *Ardea cinerea* and *goliath*; similarly only the blue definitive plumage of *Egretta caerulea* is shown, although the white-to-blue plumage sequence of this species is unique.

The authors have given special attention in the text to the "soft part colors," which are notoriously changeable with the seasonal cycles of herons, but those in the plates do not always agree with the text descriptions. In particular, the bills of *Ixobrychus* sp. and the adjacent facial skin look as if they were painted directly from dried specimens.

The maps, gathered together in the back of the book, are well done and easily understood. However, maps are presented *only* for *Ardeola*; the "Little Egret-Reef Herons superspecies" (which unaccountably omits *Egretta thula*, surely an allospecies of *E. garzetta* and considered conspecific with it by Curry-Lindahl [1971]); *Botaurus*; the "Great Herons"; the "Tropical Night Herons" (= *Gorsachius* of this book); and "The Grey Superspecies plus the White-necked Heron." The latter map omits the breeding population of *Ardea herodias* on islands off the Venezuela coast. No explanation is given as to why maps were restricted to these groups; maps of the distributions of *Ixobrychus*, *Butorides*, and *Nycticorax*, for example, would have been highly instructive.

The authors are uniquely qualified to write a monograph on herons with an emphasis on the living birds, in contrast to earlier works that have stressed morphological characters. Mr. Hancock has travelled almost worldwide in connection with his business interests, and has taken every possible opportunity to study herons in the field. Sir

Hugh Elliott, President of the B.O.U. since 1975, is rightly described in the dust-jacket blurb as being one of Britain's most travelled ornithologists. The authors reckon that between them, they have seen in the field some ¾ of the 61 species of herons recognized in their book, and have visited all major portions of the world inhabited by herons except central Asia and New Zealand.

Turning now to the text, the species accounts are preceded by the apparently mandatory Foreword by Roger Tory Peterson, an introduction, and brief (2⅔ to 4 pages) chapters on plumage and molt, breeding, feeding, migration and dispersal (half of which is devoted to a special account of the range expansion of the Cattle Egret), and conservation (which strangely omits any possible effects of chemical pecticides). The 6½-page chapter on classification includes a species list.

The writing is highly readable and a trifle discursive; the authors are inevitably courteous even to those authors with whom they completely disagree. The rather rambling style is not obtrusive in the introductory chapters, but becomes a handicap in the species accounts. The latter are uniformly divided into 3 sections headed "Distribution, migration and habitat;" "General appearance and identification;" and "Behaviour" (the latter subdivided into "feeding" and "breeding"), with many species having a fourth section for "Taxonomic notes." However, information *within* these sections is not organized consistently, and particular facts may be difficult to find. For example, a few species accounts describe voices, but in order to make comparisons of vocal descriptions it is necessary to read the whole species account to find out whether voice has even been mentioned. Although egg measurements are given for every species, the only measurements given for the birds themselves are approximations of *total length*. These are sometimes given as a range ("The Little Blue Heron is 64–74cm [25–29in.] in length"), but just as often as a single figure ("the White-necked is nearly twice as big [as the Pied], 92cm [36in.] compared with 48cm [19in.]"). These figures can appear *anywhere* in the "General appearance and identification" section, from the first sentence to 1 of the last.

The user of this book should therefore expect to do much more *reading* than is usually necessary in a reference work. But it will often be enjoyable reading, as the frequent use of the authors' firsthand information brings a special liveliness and authentic touch to the text that is often missing in monographs that are basically compilations. Additionally, they often mention observations that conflict with their own. For example, they saw *Ardea cocoi* in Argentina "constantly . . . feeding during the day though usually in deep shade," and mention them walking "more often than not upstream," implying a riverine habitat. They then cite a personal communication from D. Mock, who has always seen *cocoi* in Venezuela feeding right out in the open, often in blazing sunshine, agreeing with my own observations in Argentina, where most *cocoi* seen were standing singly out in flooded fields, with no shade whatsoever.

The first half page of the chapter on "Plumage and moult" is a superfluous recitation of the colors found in the Ardeidae. There is no general description of typical newly hatched herons, with their long, loose natal downs, most conspicuous on the head. This diminishes the impact of the statement on p. 139 that the downy young of *Cochlearius cochlearius* is "unique in being pure grey above, dull white below and with a blackish crown lacking erectile tufts. . . ." In fact, the natal down of *Cochlearius* is so short and dense as to resemble superficially that of a duckling (see Dickerman 1971, photograph p. 13). The authors also err in stating that the Boatbill differs from other night-herons in *not* having a distinctive juvenal plumage different from that of the adult. *Egretta* is said to lack the first Prealternate molt, but this was formerly believed to be true of *Ardea cinerea* and *A. herodias* until specimens were carefully examined and the molt found to occupy the place in the cycle where it "ought" to be (Humphrey and Parkes 1963b:500). One finishes this chapter with the definite impression that plumage sequences of herons have been inadequately studied; that they are probably complicated by geographic variation; and that errors have been made in interpreting them. Although the authors cite the paper by Humphrey and Parkes (1963a) on *Syrigma*, they overlooked in that paper our discovery that the buff or tawny nuptial plumes of the Cattle Egret are *white* when they first break from their sheaths. This point was reiterated by Parkes (1978), and surely in such a readily available species this exceptional plumage phenomenon should be investigated.

The chapter on "Breeding" is a valiant but foredoomed effort to synopsize the tremendous variation among herons in nesting habits, courtship, incubation, feeding and survival of chicks, and so on. The difficulty is illustrated by a report of nest-site selection in a mixed Florida colony observed by the authors, which mentions *Egretta alba* nesting "low in the leafy understorey," a statement at variance with the detailed descriptions and measurements of Great Egret nest-sites in 2 papers published too late for inclusion in this book (Burger 1978b, McCrimmon 1978). The chapter on "Feeding" is a good summary based primarily on the works of Meyerriecks and Kushlan.

In the chapter "Migration and dispersal" the latter term is used for several rather different phenomena: (1) migratory species storm-drifted outside of their normal range; (2) normally sedentary species appearing in new areas because of drought or other unfavorable conditions; (3) "overshooting" of the breeding area by spring migrants; and (4) post-breeding wandering, often in random directions in tropical forms, and in the direction opposite to the subsequent true migration in temperate forms. The authors describe typical migration routes for the major areas of the world where migratory herons are found, a summary that would have been impossible a generation ago, prior to the growth of mass banding programs. The second half of this chapter is devoted to the Cattle Egret. It is interesting to note that the northward expansion of *Bubulcus i. ibis* in Eurasia has not been at the dramatic pace of its New World colonization, and that American writers have generally overlooked the parallel dramatic spread of *B. i. coromandus* to New Guinea, Australia and New Zealand.

In the "Conservation" chapter we learn that only 2 herons are known to have been extirpated in historic times: *Nycticorax caledonicus crassirostris* of the Bonin Islands (last seen 1889), and a supposedly flightless night-heron on Rodriguez. Oddly, about 32% of this chapter is devoted to the impact of *natural* predation, slightly more than the 29% on the history of the plume trade. It is a sign of the times that this famous devastation can be dismissed as ancient history, with a brief but adequate summary, emphasizing the astonishing recovery of virtually all of the persecuted species (with the probable exception of *Egretta eulophotes* of eastern Asia). Wetland drainage and destruction of trees, especially in the tropics, are stressed as the modern threats to heron survival. Although no case histories are given, an unfortunate example unknown to the authors is the fate of the "recently" (= 1961) discovered breeding colony of *Agamia agami* near Minatitlán, Veracruz (p. 287), which was completely abandoned due to pollution only about 4 years after its discovery, and thus about 12 years before its announcement as "new" in this book (Dickerman, pers. comm.).

The authors have made a genuine attempt to achieve a "common sense" classification of herons, based primarily on the seminal paper by Bock (1956) as amended by more recent research on particular species or groups, and by their own experience. They have been (in my view) properly cautious about accepting the more radical innovations proposed by Curry-Lindahl (1971) and Payne and Risley (1976), although they conscientiously present the findings of these and other authors with whom they disagree, explaining the reasons for their dissent. I could live reasonably well with their proposed classification, with a few exceptions. The chief 1 of these deals with the genera of night herons. Bock (1956) transferred 2 monotypic genera (*Calherodius leuconotus* and *Oroanassa magnifica*) into the genus *Gorsachius* of Asia. Payne and Risley (1976) lumped the 4 species of Bock's *Gorsachius* into *Nycticorax*, from which they *excluded* the Yellow-crowned Night Heron. Hancock and Elliott have followed Bock's concept of *Gorsachius*, thus including the African White-backed Night Heron, *leuconotus*. I cannot accept this species as a member of *Gorsachius*, of which the type, *G. goisagi*, is a strange little Asian bird with a rather bittern-like plumage pattern and a stubby bill, the shortest in proportion to size in the entire family Ardeidae. The African *leuconotus*, in my opinion, is a *Nycticorax*, although differing somewhat from the remainder of the genus (the *nycticorax-caledonicus* superspecies and *violaceus*). The juvenile *leuconotus* is enough like that of *nycticorax* to have misled an inexperienced curatorial assistant into putting a young *leuconotus* in the Black-crowned Night Heron tray. The crest shape and dorsal plumes of *leuconotus* are those of a *Nycticorax* (*Gorsachius* has no dorsal plumes at all), and its general color and pattern are reminiscent of *N. caledonicus* and are completely unlike those of the Asian *Gorsachius*. In spite of Payne and Risley's failure to find osteological differences that they considered significant, the proportions of the 2 typical *Gorsachius* are quite unlike those of *Nycticorax*, including *leuconotus*. The status of the fourth species that has been assigned to *Gorsachius*, the all but unknown *magnificus* of China and Hainan, must remain tentative until more information is available on both its anatomy and its habits.

Dickerman's study (1971) of *Cochlearius* concluded that this genus be placed in its own tribe Cochleariini to reflect the many differences (in addition to bill shape) separating it from the typical night herons. The A.O.U. Committee on Classification and Nomenclature has agreed to adopt this recommendation, rather than to leave the Boatbill, as Hancock and Elliott have, as just another night heron.

The authors follow Bock in associating (Bock having combined as a superspecies) the 3 giant species of *Ardea*: *goliath*, *imperialis* and *sumatrana*. This seems to be based entirely on large size (Parkes 1978). Whereas *imperialis* and *sumatrana*, the Asian species, may indeed be related derivatives of typical *Ardea* such as the *cinerea* superspecies, *A. goliath* of Africa seems much more likely to have been independently derived from "*Pyrrherodia*" stock, the subgenus that now includes only *A. purpurea*, the Purple Heron. Among other points of resemblance between *goliath* and *purpurea* are their ground-nesting rather than tree-nesting habits, and their scutellate rather than reticulate tarsal envelopes, characters in which they differ from *imperialis* and *sumatrana* as well as from *Ardea* in general. There are also obvious color and pattern resemblances between the Goliath and Purple herons.

In their proposed classification, the authors use the usual brackets to indicate superspecies, most of which are non-controversial. Oddly, no superspecies are bracketed within *Egretta* (although a map caption indicates a "Little Egret-Reef Herons superspecies"). Surely *E. thula*, *gularis* and *garzetta* qualify for superspecies status. The authors depart from recent classifications in considering the coastal East African *dimorpha* to be a subspecies of the Western Reef Heron (*E. gularis*), rather than of *E. garzetta*. Other classifications have listed *dimorpha*, *gularis* and *garzetta* as full species. Considering the dimorphic form as a member of the coastal *gularis* makes problematical the status of the several *inland* sight records of dark egrets, such as the one I saw among a flock of about a dozen *Egretta garzetta* at Lake Nakuru, Kenya, 1 November 1976.

Although space limitations necessitated much condensation and omission, the book provides a bibliography of nearly 1000 titles for further reference. It was most unfortunate that the proceedings of the North American Wading Bird Conference held in 1976 (Sprunt et al. 1978), a meeting attended by the senior author, were withheld from publication far beyond the date originally promised to the participants, who were asked to have their manuscripts completed for publication *before* the meeting. The wealth of data in this symposium volume should have been available to Hancock and Elliott. A good indication of the current popularity of herons as study species is the appearance already of several other major papers too late for inclusion in the monograph, such as Burger (1978a), McCrimmon (1978), Mock (1978), Rodgers (1978), and Willard (1977). Biderman and Dickerman (1978) challenge, on the basis of field observations, Mock's hypothesis (quoted in the monograph) on feeding behavior of *Cochlearius*.

The authors missed at least a few pertinent references published earlier. Among these, in taxonomic order, are Dickerman (1973), in which *Ixobrychus exilis hesperis* was shown to be invalid; Norton (1965), in which a new subspecies, *I. e. limoncochae* was described from eastern Ecuador; Blake (1977:161), in which geographic variation in size was shown in *I. involucris*; Bond (1966), in which a record of *Egretta garzetta* from Barbados, although identified and published belatedly, was shown to be the first New World specimen (16 April 1954). The "doubtful" record of *Ardea cinerea* from New Zealand was verified by Parkes (1974), and the authors also overlooked the description of the resident East Indian populations as *A. c. altirostris* by Mees (1971). Finally, in several of the "supplements" to Bond's 1956 Check-list of West Indian birds, there are discussions of the status (both as to breeding and morphology) of the Caribbean population *Ardea herodias repens*.

Omission of these references from the massive bibliography hardly detracts from the overwhelming task Hancock and Elliott have accomplished in giving the reader access to so much of the heron literature. They have produced a handsome and reasonably complete compendium of our knowledge of this family as of 1977. The present dynamic state of heron research makes it virtually certain that theirs will be the standard reference work for a good many years.—KENNETH C. PARKES.

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THE LAROUSSE GUIDE TO BIRDS OF BRITAIN AND EUROPE. By Bertel Bruun, illus. by Arthur Singer. 516 birds in color, 448 maps. Larousse and Co., Inc., New York, 1978: 319 pp. $7.95.—This is a pocket-sized field guide (soft cover) to the birds of Europe, including European Russia. Like other recent guides, the format is very convenient. On the right hand pages are colored paintings of several species, while on the facing left hand pages are brief descriptions and range maps for the same species. Thus one does not need to leaf through the book in search of corresponding sections.

This is not a new book, but a reissue by a new publisher of an older, but still useful work. It was originally published in England as *The Hamlyn Guide to the Birds of Britain and Europe* (1970). At the same time or soon after, it was published in the U.S. by McGraw-Hill as *Birds of Europe*. The present version is identical except for the title and publisher. However, the same author and illustrator published another book also called *Birds of Europe*, which was not a small field guide but a large hardcover book. This was published by Hamlyn in Europe (1969) and later (1971) by the Golden Press in New York. The large *Birds of Europe* is the same book as the small *Birds of Europe, Hamlyn Guide . . .*, and *Larousse Guide . . .*, except that it has a number of full page paintings and considerable text material not found in the smaller book(s). Most of the illustrations, however, are the same ones found in the field guide(s). In addition, these illustrations are captioned with the same descriptive material that accompanies the field guide illustrations. In other words, the large *Birds of Europe* is an expanded field guide, or perhaps the field guide is a reduced large *Birds of Europe*. It is all very confusing.—ROBERT J. RAIKOW

GRANIVOROUS BIRDS IN ECOSYSTEMS. Edited by Jan Pinowski and S. Charles Kendeigh. Cambridge University Press, New York and London, 1978: xxi + 431 pp., 60 text figs., 76 tables. $41.00—Grain-eating man has a group of bird species, often locally very abundant, which exploit his staple grain crops in every part of the world. Several of the most significant of these are in the genus *Passer* and the most important is the ubiquitous House Sparrow (*Passer domesticus*). This species is known to have occurred 10,000 to 15,000 years ago in the Near East where man first developed a sedentary agriculture based on wheat and barley, and subsequently it spread to Europe as agriculture developed. From there the House Sparrow has accompanied European man in his colonization of the Earth's temperate regions and now enjoys almost worldwide distribution. It is the only grain-eating bird which is a true commensal of man and represents "one apex" of granivory. Study of the House Sparrow and the related European Tree Sparrow (*P. montanus*) was the main impetus for this book.

The present volume is No. 12 in a projected 19 volumes synthesizing biologists' production during the International Biological Program, which ended in 1974. It is the product of the Working Group on Granivorous Birds whose major objective was an "integrated cooperative study of the genus *Passer*." The House Sparrow received most attention because of its status as a pest species in many grain growing areas and because it had already been intensively studied on several continents. Considerable data were also obtained on the other nearly world-wide species of the genus, the European Tree Sparrow. The scope of the synthesis was expanded to include information on 7 other oscines of present or potential significance as granivore commensals; the essentially Mediterranean Spanish Sparrow (*Passer hispaniolensis*), the African Red-billed Quelea (*Quelea quelea*) and the New World Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscala*), Dickcissel (*Spiza americana*), Brown-headed Cowbird (*Molothrus ater*), and Horned Lark (*Eremophila alpestris*). Other granivores among the Galliformes, Columbiformes and the Anseriformes were ignored.

The first 5 chapters of the volume combine studies of adaptability and evolution with ecological studies of population dynamics, productivity and a detailed overview of avian energetics. The remaining 4 chapters attempt an assessment of the potential impact of grain-eating birds in ecosystems by use of a simulation model, outline the difficulties inherent in devising management strategies, and discuss adaptations to granivory in birds.

Despite the fact that 11 authors contributed to this volume the theme is logically and coherently developed and the chapters are suitably cross-referenced. The book is rich in information and in stimulating ideas and insights. It is only possible to mention a few highlights. The section on avian energetics is an immensely valuable summary that may well serve as a primer on the field. Particularly noteworthy is the inclusion of a large amount of new data on metabolic rates obtained by Dol'nik and Gavrilov made available to western biologists for the first time.

Anyone contemplating a campaign against a pest species should be required to read Dyer's and Ward's chapter on management of pest situations. The difficulties of ecosystem management, the frustrating tendency for solutions to be counterproductive and the failure of direct "common sense" solutions are convincingly presented. Most valuable is their scheme for making a logical choice of appropriate management strategy. Similarly Wiens' and Dyer's use of a simulation model for impact assessment demonstrates an approach to impact studies one hopes will have wide influence. The concluding discussion on adaptive strategies of granivory is a highlight of the book. Finally any student looking for a career's work should read the brief epilogue in which the state of knowledge of bird function in ecosystems is evaluated and the kinds of information still needed are enumerated.

The book is an outstanding achievement. Students of avian population ecology, energetics, the role of birds in ecosystems and management of pest species will find it indispensible. I recommend it highly.—WILLIAM J. MAHER.

SYSTEMATICS OF SMALLER ASIAN NIGHT BIRDS BASED ON VOICE. By Joe T. Marshall. Ornithological Monographs No. 25, American Ornithologists' Union, 1978; v + 58 pp., frontispiece, 15 plates, phono disc supplement, appendices I–III. $7.00 ($6.00 to A.O.U. members).—Joe Marshall has been studying owls, especially the genus *Otus*, for a long time, and has published extensively on New World members of the genus. The present work is essentially a treatise on Asian *Otus* and their relationships to *Otus* on other continents. The only other birds included in this study are some caprimulgiforms (Podargidae, Caprimulgidae) which Marshall says were "an incidental by-product of the research" (on *Otus*). Starting with the premise that the plumage of owls and other night birds "varies geographically so that the bird is camouflaged appropriately for its regional flora while sleeping in the daytime," resulting in similar coloration for different species, Marshall's aim was to find vocal clues to the confusing taxonomy of Asian *Otus*. Stationed in Thailand for 13 years, he spent his leave time travelling widely in Asia recording night birds. Alarmed by the rapid destruction of natural forests he decided to hear and tape-record as many owls as possible rather than make detailed studies of a few species. His main contribution in this work is the presentation of vocalizations that have never been taped before. He is to be congratulated for his energy and pertinacity in getting to so many out-of-the-way places while there was still some forest left and coming back with a fine collection of recordings. An excellent disc, produced in the Bioacoustic Archive of the Florida State Museum, University of Florida, Gainesville, accompanies the text, wherein are presented both Marshall's recordings and those of other workers. Ten pages of sonagrams keyed to the recordings are included in the text.

In his discussion of the taxonomy of night birds, Marshall's guiding principle is "All taxa with the same song belong together," an assumption basic to vocalization studies. Strict adherence to this rule, however, results in some very curious distributions. Vocal division of *Otus* into those with trills or rhythmic phrases of more than 4 notes per sec and those with short songs with fewer than 4 notes per sec results in the trilling *Otus leucotis* of Africa being grouped with the New World Screech Owls and the hooting

O. flammeolus of North America being included among the Old World Scops Owls. *Otus insularis* of the Seychelles has a gruff voice remarkably similar to that of *O. magicus* on Biak, off New Guinea, and is consequently reduced by Marshall to a subspecies of *magicus*. *Otus hartlaubi* from the island of São Tomé in the Gulf of Guinea is also placed with the Indonesian species *O. magicus*. Marshall defends these far-flung distributions by pointing out that *Otus* spp. are successful colonizers of islands, and he reminds us that the type of *O. elegans* was taken on board ship in the middle of the East China Sea. While it is entirely possible, if astonishing, that *Otus magicus* should cross 7000 km of the Indian Ocean to reach Mahé Island in the Seychelles, it is almost inconceivable that it should fly around or across Africa to reach a small island off the west coast. Is this, then, a relict distribution? Marshall makes no suggestions, merely presenting us with the information. He notes that the quality of the note of *Otus hartlaubi* resembles that of *O. scops* of southern France, but apparently discards the latter as a possible relative (which would be geographically more believable) because of the long interval between notes, more charactersitic of *O. magicus*. One wonders if too much weight is not being given to a single character here.

In spite of the emphasis on voice, Marshall admits the importance of morphological criteria, and these are given a lot of space in the text. Information on the caprimulgiforms is presented in the form of morphological keys, 1 to the species of *Batrachostomus* and the other to Southeast Asia nightjars. Vocal information is given in the keys, but voice is not used as a separating character within the keys. *Otus icterorhynchus* of Africa is closely linked with *O. balli* of the Andamans and *O. stresemanni* of Sumatra on the basis of plumage alone, the voices of the latter 2 being unknown.

Whether one agrees with Marshall's ideas or not, he has certainly provided a wealth of information from which others may draw their own conclusions. This is a valuable contribution to the literature on avian vocalizations and a welcome addition to the list of published sound recordings. Especially the record is a must for anyone interested in the songs of night birds.—STUART KEITH.

SOURCEBOOK ON THE ENVIRONMENT. By K. A. Hammond, G. Macinko and W. B. Fairchild (eds.). University of Chicago Press, 1978:613 pp. $20.00.—This comprehensive work dealing with various environmental questions was initiated by the Association of American Geographers. Its goal was to "provide a broad guide to selected aspects of the environmental literature." Section 1 deals with "Environmental Perspectives and Prospects" and includes chapters on human-environment interactions, resource scarcity, the limits to growth and model ecosystems. Each chapter contains a quick review of the major research works in that particular area, and concludes with an extensive bibliography. Part 2 deals with "Environmental Modification: Case Studies" and includes chapters on the effects of industrial activity on water quality, mining and the environment, and solid waste recovery. Part 3 is concerned with the "Major Elements of the Environment" and deals with air quality, water quality, energy policy and animals in the environment. Being a zoologist, I examined the animal chapter in some detail. Ecology is covered in about 2 pages and, as might be expected, lacunae are evident. The most recent texts cited are Kendeigh (1961) and MacFayden (1963). No reference is made to the modern texts of Pianka (1974), Krebs (1978), Ricklefs (1973) and others (although Krebs is cited in an earlier chapter dealing with wildlife ecology). The author of the chapter did not realize that Dr. A. S. Romer died some years ago. In general, many of the citations deal with broad textbooks or reference works. For an ecologist, the chapter is not exceptionally useful, although it probably gives a non-ecologist a place to begin working. Thus each chapter in the book will serve as an orientation chapter to specialists in other disciplines. The last major section entitled "Research Aids" presents lists of environmental periodicals, major environmental legislation and environmental organizations.

This is a useful book for any person needing a quick reference to a variety of environmental problems. The citations will at least point up some of the major research papers published through about early 1976.—MICHAEL A. MARES.

COMPARATIVE STUDY OF TODIES (TODIDAE): WITH EMPHASIS ON THE PUERTO RICAN TODY, *Todus mexicanus*. By Angela Kay Kepler. Publications of the Nuttall Ornithological Club, No. 16, Museum of Comparative Zoology, Harvard University, Cambridge, MA, 1977: 190 pp., 8 maps, 37 tables, 65 figs., $11.75—Despite their tameness, endemism to the Greater Antilles, and many other interesting features, todies have not been studied extensively. Yet the family is an ideal subject for analyzing population regulation in tropical birds, species abundance in tropical habitats, specialization of birds on oceanic islands, and ecological equivalence. This is just what Kepler set out to do, and she does it well. The natural history of the family is documented, the niches of each of the 5 species in widely differing communities are analyzed, and the pathways of evolution are discussed.

Kepler conducted field work in Puerto Rico over a 3 year period. In order to determine the distribution, abundance, and optimum habitats of *Todus mexicanus*, to evaluate its niches in different forest communities, and to discover possible mechanisms of population regulation, she made detailed analyses of population densities in major habitat types: rainforest, moist and dry limestone forest, and Cordillera forest. Additionally, trips were made to other Caribbean islands and to South America to study other species of *Todus* and birds of related interest such as tody-flycatchers (*Todistrostrum*), motmots (Momotidae), and warblers (Parulidae).

The first 2 chapters provide a brief morphological description of the birds and detail the distribution of the family in the Greater Antilles. The major vegetation is described for a variety of habitats, especially those in Puerto Rico.

There follows an in depth study of tody behavior. Maintenance behavior is discussed. Vocalization and wing rattling are described and their function in defense and courtship are explained. Territoriality, associated displays, and vocalizations are described, as are foraging locations and microhabitats, and feeding habits, rates, and efficiency. An appendix lists food items eaten by Puerto Rican Todies with brief notes on the other species. A comparison is made with competitors and ecological equivalents such as tody-flycatchers and some warblers that also use leaf undersurfaces.

Several chapters deal with the breeding biology of todies. Burrow size, location and construction are described. Courtship displays, eggs, incubation, and the care and development of the young through fledging are carefully detailed. Kepler reports nest helpers among todies and discusses their effect on clutch-size. Food, climate, predation, territoriality, availability of nest sites, and interspecific competition are discussed as factors in population regulation.

Kepler concludes with a discussion of evolution in the family. The morphological uniformity of todies is noted and differences in size, color and behavior among the species are tabulated. Other morphological, behavioral and developmental characters are considered, and it is concluded that todies are most closely related to motmots. The author postulates a short-billed Central American prototype that colonized the West Indies, speciating linearly eastward in more recent times. Evolutionary pathways among the islands are proposed. The 2 sympatric Hispaniolan species are shown to have diverged from other forms of *Todus* and from each other in morphology and behavior. Courtship displays, vocalizations, feeding and habitat separation serve as isolating mechanisms.

This monograph is well-written and almost devoid of errors. A White-fronted Nunbird (*Monasa morphoeus*) (p. 137) is termed coraciiform. No citation is given for *Paleotodus emryi* (p. 47) until much later in the book. This study is an excellent blend of ecology, ethology and morphology, and deserves to be read as a notable field study of an interesting and unique family.—DAVID R. MAURER.

BIRD FAMILIES OF THE WORLD. By C. J. O. Harrison (ed.), illus. by Ad Cameron. Harry N. Abrams, Inc., New York, 1978: 264 pp., over 500 color illustrations. $25.00.—All the families of living birds and major fossil families as well are surveyed in this large-format (9 × 12 in.), copiously illustrated work. Each family is discussed in some detail with an introductory section covering appearance and size, and additional sections dealing with distribution, feeding, nesting and the young, behavior, and composition (taxonomic relationships). For some groups other sections are also given, such as economic importance. The sections vary in length, but may be up to several paragraphs long, and considerable information is thereby provided. More than 40 different authors have contributed articles about families with which they are especially familiar, so the text as a whole has an authoritative ring to it. At the same time the accounts are not highly technical, so the work is appropriate for students and interested nonprofessional ornithologists. Despite the multiple authorship, however, a common style is followed throughout, giving the book continuity and coherence.

In spite of the obviously careful editing, a number of errors and unfelicitous statements have crept in. Most frequent are misspellings of scientific names, especially in figure legends. Examples are *Scopus umbrella* (for *umbretta*, p. 51), *Ephippiohynchus* and *Ephipphiorynchus* for *Ephippiorhynchus* (p. 52), and *Laniarus* for *Laniarius* (p. 197). The Andean and James' flamingoes are said to lack a hallux (p. 56), but in the illustration on p. 55 have re-evolved these lost structures. In the figure on p. 60 the Hooper and Coscoroba swans have their identifying numerals reversed. Parrots are defined as birds in which the upper mandible "articulates with the skull" (p. 120). This presumably refers to their especially conspicuous cranial kinesis, but is true of birds generally.

The many color illustrations by Ad Cameron are a major contribution to the book. One of their purposes is to show variation among the members of a family, so in each case a number of species are drawn so that differences in their plumages, bills, etc. may be readily compared. Another purpose is to illustrate typical or unusual behaviors, so instead of the usual static depictions of birds perching or standing around idly, we see them feeding, courting, carrying food, giving various displays, building nests, and so on.

The birds are lifelike and realistic for the most part, though in many cases the heads and bills appear a bit too large.

These criticisms are minor. Altogether this is an excellent survey of the birds of the world, and is highly recommended. Considering the absurd prices of some books today, this volume is an excellent value.—ROBERT J. RAIKOW.

STATUS AND DISTRIBUTION OF ALASKA BIRDS. By Brina Kessel and Daniel D. Gibson. Studies in Avian Biology, No. 1, Cooper Ornithological Society, 1978: 100 pp., 1 map, 2 tables, 7 photographs. $8.00.—This is the first in a new series of monographs published by the COS for papers too long to include in *The Condor.* It replaces the previous series, *Pacific Coast Avifauna,* and is intended to broaden the range of subjects eligible for publication. This first number, however, is quite in keeping with the more limited goals of the old series. It is a compilation of data on the distribution of birds in the largest state, and their status in regard to abundance, breeding activities, and so forth. Of 381 species that have been recorded in Alaska, 202 are discussed in detail in this work. The remainder are adequately treated in previous publications.—R.J.R.

THE CALIFORNIA QUAIL. By A. Starker Leopold, illus. by Gene M. Christman. University of California Press, Berkeley, 1977: 281 pp., 1 color plate, 4 range maps, 95 numbered text figs., 40 tables. $14.95—The name Leopold has become synonymous with the cause of conservation in North America. This family has probably done more than any other in educating the American public in the principles of wise use of our natural resources and the concept of a "land ethic." A. Starker Leopold's book on the California Quail continues this tradition. It was written primarily as "a stimulus and guide to the preservation and management of the California Quail." But in so doing Leopold has managed to tell his readers a great deal about this bird, its habitat requirements, and the impact that man has had on both its distribution and abundance.

The book is divided into 3 parts: "The Bird and Its History," "Natural History," and "Quail Management." The first deals with the bird's historical distribution and the flow and ebb in abundance with the settlement of its range by Europeans. As with so many avian species in North America, the California Quail appears to have benefitted greatly by the first agricultural pursuits of these immigrants. The initial increase in heterogeneity of the environment, as the result of grazing and tilling small plots, undoubtedly provided a much enhanced habitat for this bird, allowing it to increase in numbers, probably to levels never before realized and, as Leopold points out, unlikely ever to be achieved again. This is because the small grazed and tilled plots have been expanded, destroying the intervening quail habitat, to become vast expanses of farmed land devoid of habitat usable by this bird. It is here that one senses Leopold's frustration with his fellow North Americans and their general lack of a resource conscience. He discusses a fundamental paradox in our land tenure system that continues to frustrate individuals and agencies concerned about the future of our native flora and fauna. He states that there "is a paradox in the legal basis for conservation of resident game species . . . In the State is vested ownership of the game and responsibility for its management. Yet the State is largely powerless in exercising the on-the-ground husbandry required to maintain a suitable habitat where the species can exist." Usually in the "process of land-use decision making, the [State] plays a minor role or none at all. Yet the [State] is nominally the custodian of wildlife." Is it not time that we in North America attempted to do something about this paradox?

The second part of the book summarizes the studies that Leopold and his students have undertaken to interpret the morphological, physiological and behavioral adaptations that this magnificent little bird shows to the range of habitats it occupies. For me, the most exciting chapter is that dealing with the impact of rainfall on reproduction. This species seems very well adapted to respond to any change in precipitation which, over most of its range, is the 1 environmental factor of overriding importance. The apparent feedback of plant chemicals, themselves controlled by available soil moisture, on the reproduction of this bird, would appear to be a very elegant mechanism for population regulation. It needs to be studied in greater depth in this species and in others occupying such habitats. Another aspect of this bird's biology that would seem to promise great rewards to the patient observer is that of dominance relationships among birds in broods, within coveys and between coveys. It is unclear to what extent dominance and dispersal are important phenomena in the dynamics of populations of this bird.

The third section deals with practical suggestions for the improvement of quail habitat. It is directed primarily, I would think, towards the holders of private estates, mainly ranchers who may be the most sympathetic to Leopold's suggestions. Leopold's advice seems both realistic and appropriate, albeit somewhat piecemeal and often of transitory usefulness, no doubt because this bird's position in community succession is one associated with what can be considered pioneer stages. At times I felt the material presented here had already been dealt with adequately in other sections, for example, the need to create or maintain cover near water. This is stated in various ways several times. Perhaps, however, Leopold thinks this is a point that needs to be impressed upon the reader. I also found Appendices A (by Nissen) and C (by Erwin) very anticlimactic. If Erwin's material is significant, why wasn't it published elsewhere?

The book is attractively put together, liberally illustrated with figures in the text and pleasing sketches by Christman heading each chapter. Christman's color plate, reproduced on the dust jacket, is very attractive indeed. The text is virtually free of typographical errors (I found only 2) and the graphic material is generally good (Fig. 50 has been printed on its side and Fig. 68, upside down). The photographs, although presumably depicting adequately that for which they were chosen, would, I suggest, not meet with the approval of California's tourist agencies!

Hopefully, this book will spark considerable interest among land managers throughout the range of the California Quail, and prompt them to set aside habitat for this species. The lessons provided in this book also have applicability throughout North America and beyond; one can substitute any species for the quail and apply the same principles expounded here equally well. The second section of the book will appeal to ornithologists in general in its summation of the salient data on the biology of this bird. The many, as yet unanswered, questions about "the natural controls over population numbers in this fascinating species" should stimulate us to further research efforts.—DAVID A. BOAG.

THE ECOLOGY AND BEHAVIOR OF THE PRAIRIE WARBLER *Dendroica discolor*. By Val Nolan, Jr. Ornithological Monographs No. 26, 1978; xxii + 595 pp. American Ornithologists' Union. $29.50.—It is appropriate that this volume bears a dedication, in addition to the author's wife, to the late Margaret Nice, because it is inevitable that this book will be compared to her classic "Studies in the Life History of the Song Sparrow." For years her 2 volume work stood as a model of thoroughness in the study of the life history of a single species. When announcing the imminent publication of the Nolan work at the 1978 meeting of the American Ornithologists' Union, the editor, John William Hardy, commented that it now represents the most complete life history study of any bird. After reading it, I agree.

Nolan studied Prairie Warblers near Bloomington, Indiana intensively from 1952 to 1965, and made additional incidental observations to 1972. He worked on 2 tracts of land measuring a total of 100 ha. Analysis of the data and reworking of the text extended into 1976, so the book covers a considerable period of field study and analysis.

The book contains 41 chapters covering such topics as the Prairie Warbler in winter, spring migration, various aspects of behavior during the breeding season, clutch-size, eggs, development of the nestlings, the mating system and sex ratio, interrelations between the Brown-headed Cowbird (*Molothrus ater*) and the Prairie Warbler, reproductive success and recruitment from reproduction, survival and mortality, population structure, and, finally, plumages, measurements and molts; in other words, just about every aspect of Prairie Warbler life history. There are 9 appendices detailing present breeding range, descriptions of breeding habitats, winter habitats, simulation of reproductive success of a hypothetical Prairie Warbler, plumage color details, pterylosis, miscellaneous anatomical and physiological data, and scientific names of organisms referred to in the text.

Most of the material is highly quantitative. There are 186 tables of quantitative data, and most of the 42 figures illustrate statistical analyses. Descriptions of maintenance and comfort behavior are mostly qualitative, but descriptions of courtship behavior, for example, are rather heavily quantified. Although these descriptions are very detailed, drawings of the birds in the various display postures would have helped the reader to envision them. Overall, the author has gone to great lengths to apply statistical treatment to his observations in order to analyze and interpret them.

I found particularly interesting the chapter detailing behavior during pair formation. In my own experience it is very difficult to observe the first encounter of male and female passerine birds on territory in the spring, because it is an unpredictable occurrence, and requires that the males be kept in view for long periods of time in anticipation of the encounter. That Nolan was able to observe what seemed to be the first encounter of several mated pairs is an indication of the amount of time he spent in observation.

Also of interest was his documentation of long distance movements (up to 1 km) of males and females off territories that they had occupied early in the breeding season. Some males simultaneously held 2 different territories, sometimes contiguous, but sometimes separated by extensive natural boundaries. Males also moved considerable distances from their territories as "explorers." Nolan suggests that what have been considered a "floating surplus" of males in some species may actually be explorers.

It has usually been the accepted procedure in describing the behavior of a species to provide a general synthesis of the various individual behaviors; the range of variation is described, of course, but individuals are not often analyzed in detail. Nolan presents a great deal of detail on specific individuals. This practice illustrates clearly to the reader the degree to which individual birds differ among themselves, but it does make for more tedious reading. A good example of this presentation of detailed individual data is found in Table 62. This table is entitled "Some measurements of eggs of selected females." Nolan presents data for length, breadth, volume and elongation of eggs from each of 6 females, all at least 2 years old, that had at least 2 clutches. I question the value of this much individual detail, and would have been satisfied with the summary table, also provided, which includes all eggs measured. Besides the table on variation among old females, and the summary table, there are tables of egg characteristics according to the order in which laid, and according to age of female.

Because of the great amount of detail presented, the reader becomes aware of a rather high degree of repetition. For example, on p. 125, Nolan presents data on nest weights according to date, and attributes the greater bulk of first nests to a need for better insulation early in the season when temperatures are lower. Again on p. 155 in a section on the duration of nest building, he discusses nest size, climate, and duration of building, and reiterates that early nests may be bigger, and for that reason take longer to build, because it is adaptive to install more insulation against cold. Because the topic naturally comes up during the discussion of different aspects of the general subject of nest building, I am not sure it is possible to avoid the repetition, but it does prove mildly annoying when encountered.

It is a little disconcerting in this otherwise extremely quantitative and precise work to encounter the rather vague sentence (p. 203), "I passed numerous other nests at dark on the day before laying of the final egg, and females were probably always present." Likewise, on p. 316 the statement "stretching of one wing and then the other probably was observed once." These indefinite and poorly supported statements seem out of place to me. It would have been better to omit such bits of information rather than pursue the goal of completeness to the point of including tenuous data. Perhaps David Lack was going too far when he decided (Life of the Robin, 1953) to include only those actions seen on at least 6 occasions, but it does seem justifiable, and desirable, to include only those actions seen clearly and surely.

Nolan was not content merely to observe the presumably undisturbed behavior of Prairie Warblers on his study area, but he also tried various experimental procedures including manipulation of nests during construction, and of the number of eggs and young in nests in order to ascertain the response of adults to different conditions. These manipulations enabled him to fill in some details of behavior that would not otherwise have been available, and also to interpret the factors underlying certain behaviors.

Perhaps 1 of the most significant sections of the book is the chapter on the Brown-headed Cowbird and its effects on Prairie Warbler populations. Nolan points out that "The simple and direct way to investigate the impact of the cowbird would be to compare production of female Prairie Warblers that escaped parasitism for a full season with that of the female population as a whole." He feels that this method cannot be used in this study "because information is incomplete for the many females that built one or more nests too high to inspect or spent only part of the season on the study area." In order to analyze the effects of cowbirds on Prairie Warbler populations he therefore calculated the production of hypothetical warbler populations, using simulation, and plugging in data obtained in the field. The simulation suggests that the Brown-headed Cowbird lowered the warbler's production by 13.3%. Comparing his actual observation of production of fledglings per nest with his simulated results, he finds 2.16 warbler fledglings per nest in the real population, and 1.96 in the simulated population, vs. 2.26 in a simulated, unparasitized population. The very fact of carrying out the simulation is impressive, but it is difficult to evaluate it. Is it really worth all the effort? Are the results from the simulated population really more accurate, that is, do they reflect reality better than the rather incomplete field data? It is hard to be sure.

There is an incredible amount of information packed into this book. Having attempted to observe many of the life history details of other species that Nolan describes for the Prairie Warbler, I find it amazing that he was able to observe as much as he did during his study period. There is no question in my mind that, despite a few minor flaws, the book represents an important milestone, setting a new standard for life history studies of birds.—WILLIAM L. THOMPSON.

OBSERVATIONS ON PELAGIC BIRDS IN THE SOUTH ATLANTIC OCEAN IN THE AUSTRAL SPRING. By Maurice A. E. Rumboll and Joseph R. Jehl, Jr. Trans. San Diego Soc. Nat. Hist., 19(1):1–16, 1977. 12 Figs., 1 table. No price given.—A study of seabird distribution between Tierra del Fuego (53°S) and southern Brazil (29°S) in 1975.—R.J.R.

APPENDICULAR MYOLOGY AND RELATIONSHIPS OF THE NEW WORLD NINE-PRIMARIED OSCINES (AVES: PASSERIFORMES). By Robert J. Raikow. Bulletin of Carnegie Museum of Natural History, No. 7, 1978: 43 pp., 5 tables, 10 figures. $3.50.—The gross morphology of the forelimb and hindlimb muscles was studied in approximately 100 species of songbirds, and analyzed cladistically to construct a phylogeny of the New World nine-primaried oscines. Methods and problems of cladistic analysis are discussed, and the rationale for the proposed phylogeny is presented. The Vireonidae are excluded from the assemblage. The Parulidae are the most primitive family in the group, the Thraupidae somewhat more advanced, but possibly polyphyletic. The Icteridae may be sister group to the Emberizinae, with *Spiza* as a link. The Drepanididae arose from the Carduelinae. The position of various problematic genera is discussed. A noncladistic classification is presented that does not depart greatly from current concepts.—R.J.R.

ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION. VOL. 14. BIRDS OF THE LAKE MICHIGAN DRAINAGE BASIN. By George J. Wallace. Argonne National Laboratory, Argonne, IL, 1977: 112 pp., $5.50 (paperbound), $3.00 (microfiche).—Order from National Technical Information Service, U.S. Dept. of Commerce, 5285 Port Royal Road, Springfield, VA 22162.

OWLS BY DAY AND NIGHT. By Hamilton A. Tyler, illus., by Don Phillips. Naturegraph Publishers, Inc., Happy Camp, California, 1978: xii + 208 pp., 16 color plates, a few black-and-white photos, many halftones and black-and-white drawings, 9 tables, 18 range maps. $6.95 paper, $11.95 cloth.—Although low priced, this is one of the more useful books on the market today for the beginning student of the natural history of North American owls. It is the intent of the author not simply to describe each of the 18 species of owls found in North America, but to illustrate and discuss each species in a manner that emphasizes the differences between, as well as the particular uniqueness of, the various species. On the whole, he has succeeded.

Part I contains 6 chapters that introduce the reader to "owlness" and describes the general traits shared by all strigiforms. Included in some detail are the distributions of each species (illustrated by range maps) tabular descriptions matching species with habitat-types, and discussions of raptorial lifestyle, with special emphasis on the beneficial aspects of predation. Feeding behavior and pellet formation, the general response of potential avian prey species to owls (mobbing), species-specific vocalizations, nesting behavior, and a short history of American Indian lore concerning owls are also discussed.

Part II contains 2 chapters that together are subdivided into 20 sections. The first chapter has 1 section devoted to the characteristics of the Tytonidae and 1 to *Tyto alba.* The second chapter covers the Strigidae and its 17 members. Each species account begins with a halftone of the owl under consideration, its common and scientific names, range, and body size. Then, approximately 5 pages of text are used for discussing such topics as feeding and reproductive behavior, morphology, nesting, and personal experiences of the author with the species. The book ends with a short afterword by the author, a listing of alternative common names for each species, the Latin and Greek meanings of the generic and specific names, a list of references for further readings, and an index.

As with all such efforts there are some dogmatic statements, anthropomorphisms and a few outright errors (i.e., ". . . the Burrowing Owl makes no distinction at all between night and day . . ." p. 42, "Some small owls take special pains to conceal themselves by projecting calls with a ventriloquial effect . . ." p. 44, both male and female Burrowing Owls sing, p. 137, and "The pitch of an owl's hoot, for example, depends upon the diameter of air passages, and that in turn depends on the size of the bird." p. 53). However, most of these commissions are rather minor and already so well ingrained in the general avian literature that they will probably never be uprooted. Major failings of the text are few: state boundary lines are excluded from the range maps, greatly reducing their usefulness, and much of the recent literature concerning a variety of topics has been ignored. For example, the most recent citations of research on vision and hearing are Dice (Am. Nat. 79:385–416, 1945) and Payne (Living Bird 1:151–159, 1962), respectively. However, examples such as the latter are not too serious inasmuch as the focus of this book is on general natural history rather than the specifics of anatomy, physiology, etc.

The illustrations by Phillips are generally poor and are not alone of sufficient quality to warrant the purchase of this book . . . even at $6.95! Most photos are blurry or simply "bad shots." Line drawings are not exceptional, while the halftones are small and of a quality equaled by many other works. The color plates are inferior to almost any others I have seen. Size relationships among the owls and the other animals in the paintings are often inaccurate. Colors, particularly those of the facial region, are over-done (especially red). Habitat settings for the owls are inappropriate at times. *Otus trichopsis* in Plate III sits atop an *Opuntia* sp. with Mesquite (*Prosopis* sp.) in the background, while the text states correctly that the species' habitat is "pine-oak."

This book contains much more information than a field guide and, as its length necessitates, considerably less than that found in the Bent series. The high points of the natural history of each species of owl, however, are well covered by Tyler and they are presented in an interesting and easily digestible manner. Its size is about right (14 × 21 cm) for the bookshelf, the dash of the car, or one's 60/40 coat pocket; its price is definitely right in today's climate of escalating publishing costs. I recommend this book highly to all beginning students with inclinations toward learning more about owls. —DENNIS J. MARTIN.

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Manuscripts.—Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced (*especially tables and "literature cited"*), with at least 3 cm margins all around, and on one side of good quality paper. Do not use eraseable typing paper. All pages should be numbered. Three copies should be submitted. Xerographic copies are acceptable if they are clearly readable and on good quality paper. Copies on heavy, slick paper, as used in some copy machines, are not acceptable.

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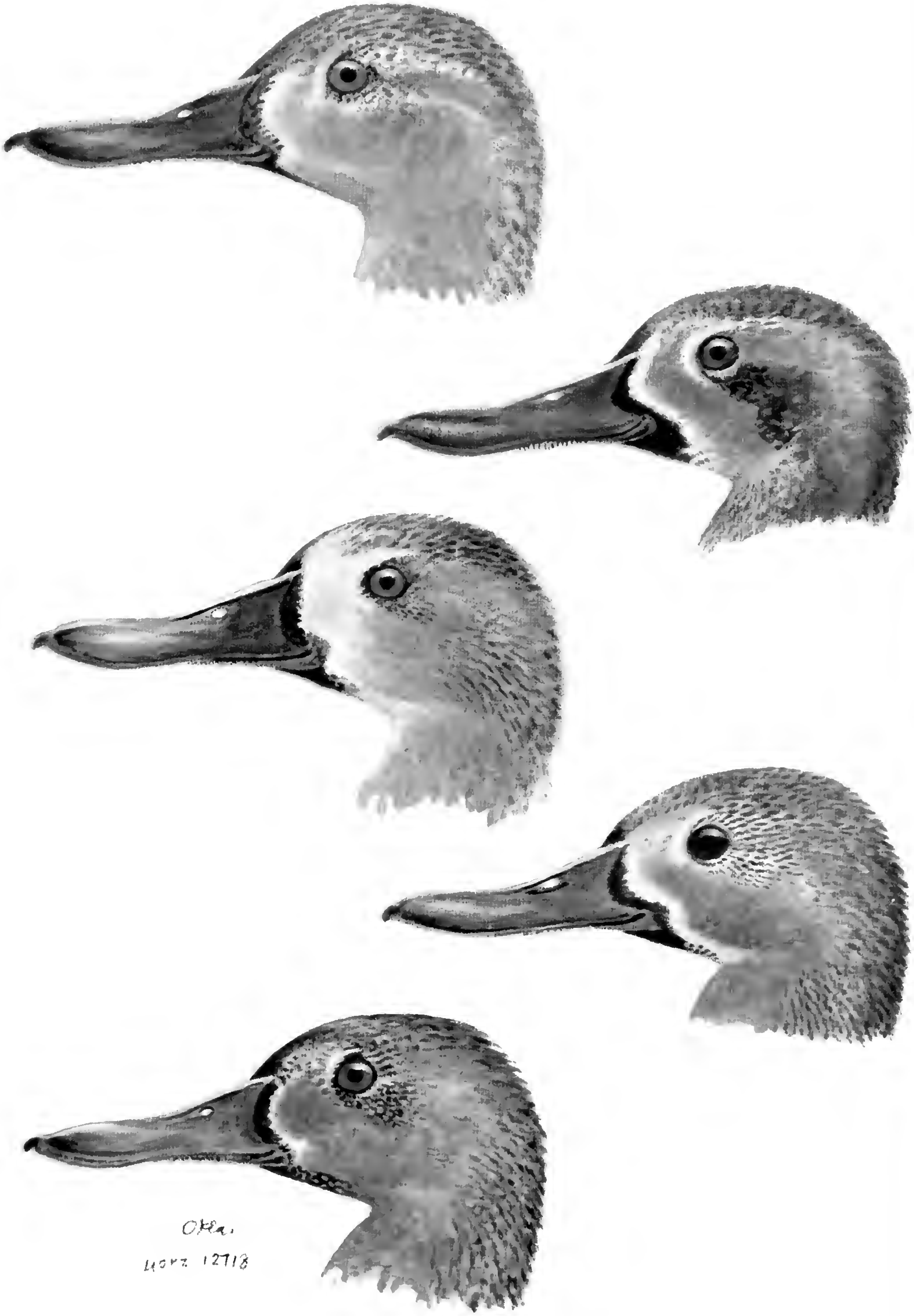

Drake Blue-winged Teal X Cinnamon Teal Hybrids.
Watercolor from prepared specimens by George Miksch Sutton.

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BLUE-WINGED × CINNAMON TEAL HYBRID FROM OKLAHOMA

ERIC G. BOLEN

In their classic revision of the Anatidae, Delacour and Mayr (1945) recognized use of a broad spectrum of biological features to determine phylogenetic relationships. For example, behavioral data were considered in addition to the more traditional anatomical and plumage characteristics of ducks, geese and swans in determining tribal affinities and the appropriateness of combining genera. The occurrence of hybridization provides insight into the closeness of relationships among birds (Sibley 1957), especially among anatids where more hybrids are known than in any other avian family (Johnsgard 1960). Gray (1958) has recorded about 400 waterfowl hybrids.

For 2 species of the blue-winged ducks (*Anas*, Anatini) of North America —the Blue-winged (*Anas discors*) and Cinnamon (*A. clypeata*) teals—the females are essentially indistinguishable and their breeding ranges are partially sympatric. Detection of hybrids of these species, while known from avicultural records (cf. Gray 1958), has therefore been limited.

For several decades notes in the literature have described, in varying degrees of completeness, male hybrid Blue-winged × Cinnamon teals from the wild. In the course of borrowing these specimens, an additional hybrid was located in Utah that had not been described in the literature; this bird and others in collections were examined and described elsewhere (Bolen 1978) except for a bird prepared as a taxidermist's mount (good description in Harris and Wheeler 1965). The Frontispiece, by George M. Sutton, portrays for the first time details of the facial features of the 4 available hybrids previously described in the literature plus a more recent hybrid from Oklahoma.

OKLAHOMA SPECIMEN

At Lake Overholser, Oklahoma Co., Oklahoma, a male Blue-winged × Cinnamon teal hybrid was taken by John D. Newman on 10 March 1977, and

TABLE 1

MEASUREMENTS FOR 5 HYBRID MALE BLUE-WINGED TEAL × CINNAMON TEAL

	Locale				
Measurements	Texas[a]	Utah[b]	Utah[c]	California[d]	Oklahoma[e]
Total length	379	336[1]	374	407	387
Tail	65	47	72	—	61
Wing	183	178	186	183	193
Exposed culmen	48	43	40	48	42
Greatest width of culmen	18	17	16	19	17
Tarsus	30	30	31	—	32
Middle toe	38	35	36	—	38

[a] Bolen (1978); Welder Wildlife Foundation Museum No. 2081.
[b] Wilson and van den Akker (1948); Univ. of Utah Museum Zoology No. 22203.
[c] Bolen (1978); Univ. of Utah Museum Zoology No. 17474.
[d] Harris and Wheeler (1965); Humboldt State College No. 957.
[e] Previously unreported specimen; Univ. of Oklahoma Stovall Museum No. 12718 and G. M. Sutton No. 16280.
[1] Neck of this specimen foreshortened in preparation of skin.

presented to George M. Sutton for preparation and accession in the University of Oklahoma Museum (No. 12718). Standard measurements for the Oklahoma hybrid are generally similar to those reported elsewhere (Table 1).

Facial features include the prominent black chin extending 12 mm posterior to the lower mandible, a characteristic that seems distinctive among each of the hybrids I have examined. The white crescent, perhaps the most obvious feature of males suggesting hybridization in these species, is an 8 × 3 mm marking anterior to the eye, faintly connected to a 1–2 mm wide line paralleling the bill's margin; the white facial marking extends just over the eye and thereafter diminishes into the darker occiput plumage. The white facial plumage of the hybrids, although clearly present, is highly variable in its location and extent (see Frontispiece). Harrison and Harrison (1971) have shown that among certain blue-winged ducks, the white facial crescents appear as a result of hybridization via heterophoric reverse mutation; this feature becomes a dominant recessive in hybrids involving the Northern Shoveler (*A. clypeata*), Red Shoveler (*A. platalea*), and Cinnamon Teal, each without white crescents in the adult male plumage.

The Oklahoma hybrid has the prominent black spotting on the upper breast, abdomen, and flanks typical of a drake Blue-winged Teal. These markings are present, but in varying degrees of prominence, among the other hybrids examined earlier (Bolen 1978). In all 5 specimens, the breast and abdominal plumage is clearly dominated by cinnamon coloration.

The prominent white flank marking of male Blue-winged Teal varied among the 5 hybrids from conspicuously "light" in the California birds (Harris and Wheeler 1965) to tan in the Texas specimen (Bolen 1978). This marking was distinguishably whitish in the Oklahoma hybrid but washed with a cinnamon cast.

Blue-winged Teal males generally have shorter bills (range 39–45, $\bar{x}$ = 42 mm, Palmer 1976:463) than do Cinnamon Teal males (range 44–47, Palmer 1976:483), but the culmen lengths of all 5 hybrids overlapped any species-specific distinctions. Lamallae in the Oklahoma hybrid, as in the others, were well developed and prominent laterally along the proximal ½ of the bill.

Iris coloration is difficult to describe or represent pictorially since only the examination of fresh specimens enables accurate artwork. Some of the available literature mentions iris coloration (". . . reddish, fading to yellowish at the outer edge," Harris and Wheeler 1965) of freshly collected specimens whereas others do not (Wilson and van den Akker 1948). George M. Sutton examined the Oklahoma hybrid and described the iris as orange-brown. Palmer (1976:467) described the iris of Blue-winged Teal as dark gray-brown and those of Cinnamon Teal as orange or scarlet after 8 weeks (Palmer 1976:486). Since this feature is variable among Blue-winged × Cinnamon hybrids, immediate attention should be given to determining iris coloration whenever new specimens are obtained.

Finally, the Oklahoma specimen represents the easternmost record in the known distribution of Blue-winged × Cinnamon hybrids. Whereas Blue-winged Teal are found throughout much of North America, including a major migration corridor through eastern Oklahoma (Bellrose 1976:278, map), the Cinnamon Teal is predominately a western species with major migration corridors in the Pacific Flyway and western Central Flyway (Bellrose, 1976: 289, map).

I am indebted to George M. Sutton for his review of this manuscript and for his usual artistic excellence in preparing the accompanying illustration for the Frontispiece.

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DEPARTMENT OF RANGE AND WILDLIFE MANAGEMENT, TEXAS TECH UNIVERSITY, LUBBOCK, TEXAS 79409. ACCEPTED 20 FEB. 1979.

COLOR PLATE

The color plate Frontispiece of the Blue-winged × Cinnamon Teal hybrid has been made possible by an endowment established by Dr. George M. Sutton.

Wilson Bull., 91(3), 1979, pp. 371–383

AGGRESSIVE BEHAVIOR IN WINTERING DARK-EYED JUNCOS: DETERMINANTS OF DOMINANCE AND THEIR POSSIBLE RELATION TO GEOGRAPHIC VARIATION IN SEX RATIO

Ellen D. Ketterson

Dark-eyed Juncos (*Junco hyemalis*) residing in central and eastern United States during winter exhibit clinal variation in sex ratio: the percentage of females increases with decreasing latitude from a low of approximately 20% in northern states to a high of about 75% in Texas (Ketterson and Nolan 1976). Similar cases of geographic variation in winter sex ratio have been described in other avian species (Nice 1937, Lack 1944, King et al. 1965, and references cited in Ketterson and Nolan 1976).

Since energetic and other costs of migration presumably increase with distance traveled, it is interesting to inquire about compensating benefits that may accrue to the average female in her more southerly wintering grounds. One obvious possibility is a lessening of intersexual competition during the season when the sexes are not required to reside together and food is likely to be in short supply (Selander 1966, Balph 1975, Ketterson and Nolan 1976).

Recent studies indicate that among captive flocks, male juncos tend to dominate females (Balph 1977) and dominance improves survivorship (Baker and Fox 1978). If food has been limiting and males have tended over evolutionary time to dominate available resources, this may account for the longer migrations of females (Ketterson and Nolan 1976, Gauthreaux 1978). The purpose of the present paper is to corroborate male dominance in free-ranging flocks and to report on other determinants of dominance.

METHODS

The flocks.—Individually marked free-ranging juncos were followed at 2 suburban locations in Bloomington, Indiana, 1 flock during each of the winters of 1971–72, 1972–73, 1973–74. Birds were caught in potter traps, banded with USFWS numbered bands and colored plastic leg bands, weighed (nearest 0.1 g), measured (flattened wing), and aged by the method of skull ossification. Those hatched in the preceding breeding season are referred to herein as immature, those hatched in an earlier year as adult. Skull ossification is a reliable index of age in this species until approximately 1 January at Bloomington (V. Nolan, pers. comm.). Birds first caught after 1 January and possessing completely ossified skulls were categorized as age unknown. Sex was determined as described by Ketterson and Nolan (1976, accuracy ≥95%).

The sex–age compositions of (1) the flocks banded each winter and (2) the sets of birds later observed in aggressive encounters are shown in Table 1; proportions are similar

TABLE 1

SUMMARY OF BIRDS BANDED AND BIRDS INVOLVED IN AGGRESSIVE INTERACTIONS

	Males			Females				
Birds banded	Im	Ad	Not aged	Im	Ad	Not aged	% male	% Im[b]
1971–72	13[a]	2	11	6	1	4	70.3	86.4
1972–73	17	9	6	6	2	4	72.7	67.6
1973–74	19	16	6	12	3	1	71.9	62.0
Birds observed in aggressive interactions								
1971–72	8	2	5	5	1	4	60.0	81.2
1972–73	13	5	0	7	2	0	66.7	74.1
1973–74	6	4	1	3	1	0	73.3	64.3

[a] Numbers given are absolute frequencies except where percentages are indicated.
[b] Percent immatures considering only birds of known age.

to those found by V. Nolan (unpubl. data) who has examined several thousand juncos near Bloomington over the past 15 years.

Observation, behavior, scoring.—From a window 3–7 m distant I used binoculars to observe juncos feeding at heavily baited (cracked corn and commercial wild bird seed), roughly circular feeding areas, 1–1.3 m in diameter. Counting only the time when juncos were present, approximately 100 h were spent in observation.

Each observed encounter in which both participants were individually identified was assigned to one of 4 categories: displacement, tie, withdrawal, and aerial chase. During displacements (see Balph 1977, pecking attack), 1 bird oriented towards another and advanced; the other quickly moved aside or left the feeding area. Occasionally the attacked bird did not yield, but turned to face the initiator until one or the other retreated. These episodes were also classed as displacement and the individual that eventually retreated was the loser. Infrequently both birds retreated after a prolonged encounter, with no apparent winner or loser. I called these ties and arbitrarily recorded ½ of a win for each participant.

Often a junco maintained its distance from others by hopping aside or ahead at another's approach, even though the other bird had not oriented or run in its direction. Such obvious avoidance behavior was classed as withdrawal, and the withdrawing bird was considered the loser (see Balph 1977, escape behavior). Finally, rapid synchronous chases occurred in which the leader appeared to set the pace. These aerial chases (see Balph 1977, flight pursuits) were seen in every month of the study (November–April) and with the sexes in all possible combinations (male chasing female, female chasing male, etc.; compare Balph [1977] who concluded on the basis of a larger sample that among captive juncos, only males pursue). In contrast to the other behaviors described, aerial chases were often initiated at some distance from food. Nevertheless, they are lumped here with other food-related aggressive behaviors, because displacements occasionally escalated into aerial chases.

Data analysis.—Two approaches were employed. First, after checking for seasonal heterogeneity, I combined data across seasons and asked whether members of 1 sex, age, or size class won more encounters than expected on the basis of chance. Secondly, I fit individuals to a linear dominance hierarchy, then noted characteristics of high ranking birds. Data for this latter effort were sufficient only from the 1972–73 flock. Birds were ordered according to the following criteria (Fig. 1):

(a) Individuals involved in fewer than 5 encounters were omitted.

(b) Individuals were placed above those they displaced or aerially chased or those that withdrew from them; they were ranked below those that displaced or chased them or from whom they withdrew. Results were organized as in Fig. 1, with the smallest possible number of entries below the diagonal.

(c) Individuals that engaged in tied encounters were classed as close together in the hierarchy as possible; however, criterion (b) took precedence to criterion (c).

(d) Application of criteria (a)–(c) produced several equivalent, alternative orders. To choose among these, I selected the one showing the greatest concordance with another measure of dominance, the proportion of interactions won. Thus, birds 6 and 7 could have been interchanged on the basis of criteria (b) and (c), but bird 6 was placed above bird 7 because it won a greater proportion of the interactions in which it was involved. The degree of association between the 2 measures of dominance, rank in the hierarchy and proportion of interactions won, was therefore high (Spearman's $r_s = 0.958$, 1-tailed $P = 0.000$). In this, and in rank order correlations to follow, birds 15, 16, and 17 were all ranked as 16 because they could not be distinguished by any of the criteria used.

RESULTS AND DISCUSSION

Presence of a hierarchy.—Figure 1 indicates the existence of a nearly linear dominance hierarchy in the junco flock studied in 1972–73, and conforms with the findings of Sabine (1949, 1955, 1956, 1959). Nevertheless, rank in the hierarchy and proportion of interactions won were not completely congruous even though proportion won had been used to resolve difficulties in constructing the hierarchy. For example, bird 2 in the hierarchy won a lower proportion of its interactions than did birds 3 or 4. This finding is similar to one reported by Sabine (1959: Fig. 1, compare birds 9 and 10 with 18 and 20). High proportional losses by relatively high ranking birds could result (1) if top dominants tend to deliberately direct more attacks toward individuals ranking close to them, and/or (2) if relatively high ranking birds are more likely than subordinates to approach top dominants. I shall return to this point below.

Determinants of dominance.—Sex, age, body size, plumage coloration, and experience are all variables that might influence an individual's rank (Tordoff 1954; Sabine 1955; Marler 1955, 1956; Brown 1963; Coutlee 1967; Martin 1970; Moore 1972; Rohwer 1975, 1977; Smith 1976; Balph 1977). These potential determinants of rank tend to covary in the junco. Data on Bloomington juncos (Nolan and Ketterson, unpubl. data) indicate that males are larger than females (as measured by wing length), and adult birds are larger than immatures (same measure, both on the average and when site-faithful indi-

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Order ct.	Sex	Age	Wing	# dom.	prop. won	Σ involv.
1		3^1			1		1^2		^{1}	3^4	1^2	1	1		^{1}		1	11	M	AD	82	10	1.000	25
2			^{1}	^{2}	2				1	1^3	2	2^2	4	^{1}		^{1}	3^4	1	M	IM	80	12	.778	45
3				^{2}	2^1				2^3	^{2}	^{1}	^{1}	^{1}			^{1}	1^1	7	M	AD	82	9	.960	25
4			↕ ^{1}		^{1}					2^1	1^1				1		2	6	M	IM	79	7	.870	23
5								2	4^1		^{2}	2	2^2	1	^{1}	^{1}	^{1}	5	M	IM	79	9	.759	29
6														1		1		8	M	IM	82	4	.857	7
7									1			^{1}					1	9	M	AD	80	3	.625	8
8																1		4	M	AD	80	1	.610	7
9										2^1	3		2		2	3	1	2	M	IM	80	7	.588	34
10									↕		1^1	1^1	1^1		1			17	M	IM	80	4	.353	34
11									↕	↕		2^1	5	1		1		12	F	AD	76	4	.482	29
12									↕	↕			2				1	10	F	IM	77	4	.200	20
13										↕				^{1}	4		^{1}	15	M	–	79	6	.310	42
14									^{1}						2	^{2}		14	F	IM	78	3	.417	12
15																		16	F	IM	76	0	.000	14
16																		3	F	IM	74	0	.000	17
17																		13	M	IM	80	0	.000	20

FIG. 1. Dominance hierarchy of 17 Dark-eyed Juncos observed the winter of 1972–73 near Bloomington, Indiana. Birds are listed in rank order with the highest rank indicated by the number 1. The wins attributable to each individual appear in the row bearing its number; the losses appear in the column headed by the same number. Displacements are represented by full-size numbers, and withdrawals are designated by superscripts; ties are indicated by double-headed arrows connecting the 2 participants. The birds are further characterized by the information in the right-hand portion of the figure. 'Order ct' signifies order of first capture relative to other members of hierarchy. 'M' signifies male, 'F' signifies female; and 'AD' signifies a bird not hatched in the preceding breeding season, 'IM' signifies a bird that was hatched in that season. Wing lengths are in mm; '# dom' signifies the number of different individuals to which a given individual was dominant. 'Prop won' signifies the proportion of interactions won and 'Σ involv.' signifies the total number of interactions participated in. Totals in the 3 right-most columns are greater than other numbers in the figure might imply, because interactions involving birds not belonging to the hierarchy were included.

viduals are measured in the year of first return). Males are more darkly colored than females (Grant and Quay 1970, Ketterson and Nolan 1976). Age also influences plumage coloration; i.e., males darken with age and adults of both sexes exhibit fewer brown-tipped feathers than immatures. With regard to prior experience at the study site, males are at least as site-faithful as females. The sex–age classes tend to arrive concurrently in the fall; if there is a difference, it is that females predominate among the earliest arrivals. Except for plumage coloration, which was not measured directly, the importance of these variables as determinants of dominance will be considered first separately, and then interdependently, where possible.

Sex.—Of 64 displacements involving a male and female, 54 were won by males ($\chi^2 = 17.15$. df = 1, $P < 0.005$, Table 2). Inspection of the hierarchy also reveals male dominance (Fig. 1). Notably, the displacements of males by females all occurred on days when snow was falling; this result concurs with Sabine's (1959) observation that "reverse pecks" were more frequent on cold, snowy days.

The question next arises, what is the impact of the intersexual dominance relationship on flock dynamics? Did males concentrate their attacks on other males and/or did females make any attempt to avoid interaction with males? In other words, were the sexes involved in a greater or lesser proportion of aggressive interactions than expected on the basis of their relative frequency in the population?

Results (Tables 1 & 2) indicate that females were participants in fewer encounters than expected (120 of the 464 participants were female, expected = 158, $\chi^2 = 9.04$, df = 1, $P < 0.005$). Further, females apparently tended not to interact with each other and male–male interaction was disproportionately frequent.

Such results might be expected if feeding position at a food source varied with dominance rank. Fretwell (1969:7), in a study of wintering juncos (of undetermined sex) in North Carolina, concluded that dominants fed close together over a circular area of baited ground, while "subdominants were more widely separated around the outside of the circle." Subordinate Yellow-eyed Juncos (*J. phaeonotus palliatus*) also feed at the periphery of the flock (Moore 1972). This feeding arrangement would cause dominants to fight among themselves to gain position in feeding areas where there were more birds than positions; subordinates would be repulsed. Although the speed of movement of juncos feeding at my baited areas made it impossible to plot position according to sex, my data would seem to indicate that near Bloomington peripheral juncos were probably female and central ones male. This could also account for the high proportion of losses accumulated by some relatively high ranking birds: males may more often contest feeding positions with central high ranking birds (other males) than with those on the periphery (females).

A study of Varied Thrushes (*Ixoreus naevius*, Martin 1970) suggests that the relationships of sex, dominance, and feeding position may not be specific to juncos. Female Varied Thrushes are usually displaced by males, but intersexual encounters occur relatively less often than male–male encounters because females appear to avoid confrontation with males by feeding at

TABLE 2

INTERACTIONS[a] OF FREE-RANGING DARK-EYED JUNCOS ACCORDING TO SEX

	O[b]	E[b]		$\frac{(O-E)^2}{E}$	
Male, male	127	101	$(.66 \times .66 \times 232)$	6.66	
Male, female	77.5	52	$(.66 \times .34 \times 232)$	12.43	$\chi^2 = 35.62$
Female, male	12.5	52	$(.34 \times .66 \times 232)$	30.06	df = 3
Female, female	15	27	$(.34 \times .34 \times 232)$	5.21	$P < 0.005$

[a] Displacements, withdrawals, ties, and aerial chases; winner's sex named first.
[b] Comparison of observed data (O) to those expected (E) on the basis of relative representation of the sexes among birds observed in aggressive interactions (Table 1).

adjacent, alternate feeding sites (see also Coutlee 1967, Glase 1973, Balph and Balph 1976).

Size.—Size is commonly associated with greater ability to defend resources (Fretwell 1972). Helms et al. (1967) have shown that wing length in juncos is significantly greater in males than females, and that wing length is correlated with lean weight.

Using wing length as an indicator of overall size, bigger juncos won a greater proportion of their interactions (Kendall's tau = 0.881, $P < 0.05$, Fig. 2). In addition, rank and wing length were significantly correlated in the 1972–73 dominance hierarchy (Kendall's tau = –0.528, $P < 0.002$). These findings corroborate those of Fretwell (1969) and Baker and Fox (1978), but differ from Moore (1972), who found no significant relationship between wing length and rank in Yellow-eyed Juncos.

Age.—Over 3 years I observed 191 ties, displacements, and withdrawals, and 0 aerial chases where the age class of both participants was known. Represented were 57 juncos; 42 of them were immature (Table 1). The interactions and their expected frequency on the basis of relative abundance of the age classes (74% immature) appear in Table 3. The immature juncos lost a disproportionate number of encounters with adults (consider rows 2 and 3, $\chi^2 = 29.01$, df = 1, $P < 0.005$), but there was no evidence that immatures avoided interaction with adults (combine rows 2 and 3, compare with 1 and 4, $\chi^2 = 2.75$, df = 2, NS).

Moore (1972) concluded that age contributes positively to rank in Yellow-eyed Juncos. Whether age is important per se, or simply appears important because it is correlated with size or some other determinant of dominance, is not known.

Experience.—Using order of capture as indicative of arrival date and therefore experience, Sabine (1959) reported that rank in her junco hierarchy

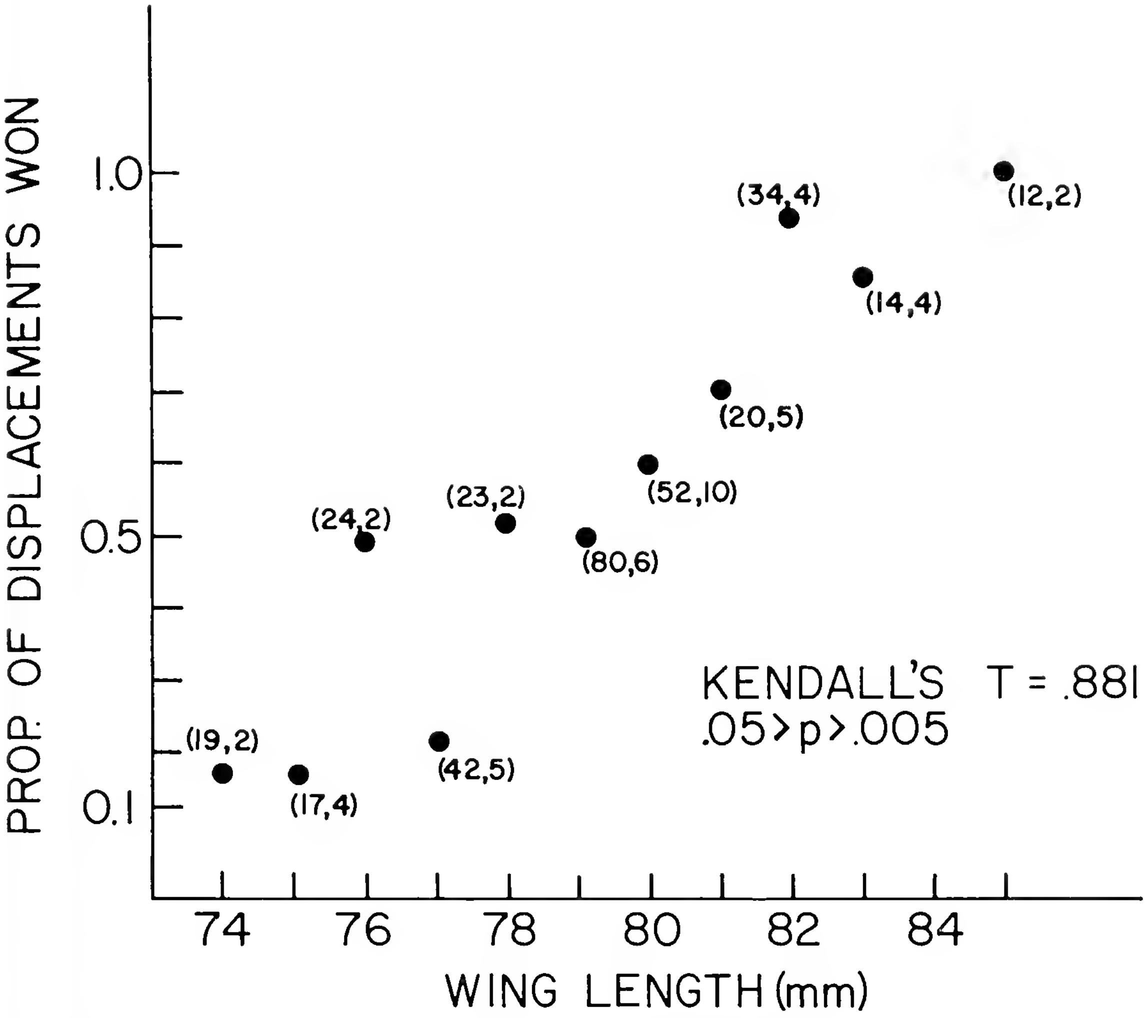

FIG. 2. Relationship between wing length (a size indicator) and likelihood of being dominant in an aggressive encounter. Each point represents the proportion of displacements won when all the displacements involving birds of a given wing length from all 3 seasons were considered. Sample sizes appear in parentheses (number of displacements, number of individuals of that wing length).

was positively correlated with experience; the earlier in the season a bird was caught, the higher its rank. I found a similar correlation between order caught and rank ($r_s = 0.472$, P = 0.028. 1-tailed).

Interactions of variables associated with dominance.—Sex, age, and wing length vary interdependently in their effect on dominance: and larger, older, male juncos appear to have the advantage.

What of the effect of each of these variables when the others are not permitted to vary? No displacements involving birds of the same wing length (by 2 mm intervals) and age but of different sex were observed, so it is not possible to test the independent effect of sex on dominance. Displacements in which the 2 participants were of the same sex and age but of different wing lengths numbered 29; 21 individuals, 5 of them females, supplied these data.

TABLE 3

INTERACTIONS[a] OF FREE-RANGING DARK-EYED JUNCOS ACCORDING TO AGE

	O[b]	E[b]		$\frac{(O-E)^2}{E}$	
Adult, adult	13	13	$(.26 \times .26 \times 191)$	0.00	
Adult, immature	65	37	$(.26 \times .74 \times 191)$	21.20	$\chi^2 = 30.12$
Immature, adult	20	37	$(.74 \times .26 \times 191)$	7.81	$df = 3$
Immature, immature	93	104	$(.74 \times .74 \times 191)$	1.11	$P < 0.005$

[a] Displacements, withdrawals, ties, and aerial chases; winner's age named first.

[b] Comparison of observed data (O) to those expected (E) on the basis of relative representation of the age classes among birds involved in aggressive interactions (Table 1).

Of these encounters, 21 were won by birds larger than their opponents, and 8 were won by birds smaller ($\chi^2 = 5.83$, $df = 1$, $P < 0.05$). When sex and wing length are held constant, only 4 displacements (involving 7 juncos) were observed between birds that differed in age. In 3 of the 4 cases an adult displaced an immature.

The correlation between rank and order of capture might spuriously arise if males, or adults, or larger birds were the first to arrive; but there is little indication that this was the case. Fourteen of the first 21 juncos caught in 1972–73 were males (67%) and 5 were adults (24%); this agrees well with the ratio of males and adults in the local wintering population (Table 1). The correlation between order of capture and wing length of birds belonging to the hierarchy was not significant ($r_s = 0.169$, $P = 0.259$), and the fit between rank and order of capture changes little when the effect of wing length is held constant (Kendall's $\text{tau}_{xy} = 0.3197$, Kendall's $\text{tau}_{xy \cdot z} = 0.2991$) (Siegel 1956).

Clearly a multivariate analysis is called for. Employing stepwise regression, I regressed proportion of interactions won by members of the hierarchy on sex, age, wing length, and order of capture, with sex and age written in as dummy variables (male = 0, female = 1, AD = 0, IM = 1). Statements of significance are not wholly appropriate, but the relative values of the regression coefficients (more accurately their *t*-values) do have meaning. The results (Table 4) indicate that among the variables considered, wing length was the most important determinant of dominance, order of capture was also important, age was less important, and sex had little influence. Together the variables explained 63% of the variation in proportion won ($r^2 = 0.633$). These findings overlap somewhat with Baker and Fox (1978) who report that wing length is a better predictor of rank than sex, plumage coloration, genotype, or measures of size other than wing length.

TABLE 4

STEPWISE REGRESSION OF PROPORTION OF INTERACTIONS WON BY MEMBERS OF 1972–73 HIERARCHY ON WING LENGTH, ORDER OF CAPTURE, AGE, AND SEX[a]

Variable	Regression coefficient	Standard error of regression coefficient	t	P	Cumulative r^2
Wing length	0.1226	0.0542	2.26	<0.045	.521
Order of capture	–0.0270	0.0133	–2.03	<0.067	.625
Age	–0.1576	0.1269	–1.24	<0.240	.678
Sex	0.1769	0.2704	0.65	<0.520	.690

Constant = –8.879

Anova: $F = 6.12$, df = 4, 11, $P < 0.008$

[a] Variables are presented in the order they were entered into the regression.

RELEVANCE TO GEOGRAPHIC VARIATION IN SEX RATIO

The foregoing findings are necessary, but not sufficient, to explain geographic variation in sex ratio in terms of intersexual competition. Although size, not sex per se, is the strongest determinant of dominance identified, the result is that females are subordinate to males where they occur together. If subordinates have lower overwinter survivorship, females should tend to overwinter separately from males.

North Carolina juncos determined in early winter to be subordinate were shown to be less likely than dominants to still be present in the same area at the end of winter (Fretwell 1969). Missing birds may have been dead or they may have moved and joined other flocks (Moore 1972:108). Such moves could affect survival, but relative survivorship of juncos making long or short moves during winter is not known. Nevertheless, independent evidence favors lowered fitness of subordinate juncos: subordinates carry less fat (Fretwell 1969, Moore 1972:112), possess larger adrenals (Fretwell 1969), feed at the periphery of the flock (Moore 1972:120), and apparently expend more energy maintaining individual distance (Moore 1972:115). Baker and Fox (1978) recently found that under conditions of restricted food availability, subordinates showed lower estimated survivorship.

Despite the foregoing, several students of juncos have concluded that subordinate birds are not ultimately prevented from feeding and so may suffer no hardship (Sabine 1959, Moore 1972, for reference to other species see Wing 1941, Dilger 1960, Kessel 1976). Under normal conditions of temperature and food accessibility, losers in aggressive encounters often simply move aside and resume feeding, and under severe conditions (low temperatures, snow and ice storms that cover food), juncos have been reported to decrease individual distance and reduce the frequency of aggressive behaviors (Sabine 1959; Pulliam et al. 1974; P. Dolan, unpubl. data). Subordinate birds apparently become more persistent in their approach to food, dominants less likely to attack.

How does dominance status influence likelihood of successful overwintering if the very weather conditions that could be critical to survival in fact suppress aggressive responses? An hypothesis is this: Under normal conditions dominants have first access to food, but subordinates too can balance their energy budgets. However, dominants may be able to lay on ample fat reserves during normal conditions, while subordinates cannot (see Baker and Fox, 1978). Several factors may prevent comparable fat deposition in subordinates. Dominants may deny subordinates access to food sufficient for fat accumulation. Alternatively, subordinates may expend more energy than dominants because they engage in more agonistic behaviors requiring locomotion (Moore 1972) or have greater basal metabolic rates as implied by their larger adrenals (Fretwell 1969). That is, subordinates may have less fat, not because they acquire less energy, but because they burn it faster.

For whatever reason, dominants are fatter (Fretwell 1969), and this fat provides the bearer with insurance against periods of high energy requirements and food shortage. In times of severe cold or prolonged snow cover, aggressive behavior may be suppressed as birds concentrate on feeding, not fighting. Nevertheless, if food intake falls short of expenditure, the fatter, i.e. dominant, birds will be more likely to survive until conditions ameliorate. Among White-crowned Sparrows, the heavier a bird at the onset of a period of fasting, the longer it can survive. Notably, males are larger than females and show greater ability to withstand fasting (Ketterson and King 1977). White-crowned Sparrows also show geographic variation in sex ratio (King et al. 1965).

Data reported herein suggest that where the sexes are sympatric, males, being bigger, should be dominant. According to the hypothesis relating dominance status to fitness, periods of high energy demand coupled with limited food accessibility would be most harmful to females. Such conditions occur most frequently in the northernmost regions of the juncos' winter range and this is the region where females are least abundant.

Complete allopatry of the sexes during winter might be expected, if intersexual dominance relations were the only factor influencing choice of a wintering site. However, size distributions of the sexes overlap, and some large females probably dominate some small males. Moreover, factors other than intersexual competition surely play a role in determining choice (Ketterson and Nolan 1976). Nevertheless, geographic variation in sex ratio probably evolved partially as a means by which females could avoid detrimental interactions with males.

SUMMARY

This paper considers determinants of dominance among free-ranging Dark-eyed Juncos visiting baited feeding stations. The data are evaluated in terms of the insight they provide into factors that may have effected evolution of geographic variation in winter sex ratio.

Dominant juncos near Bloomington, Indiana, tend to be adult males of large body size, as indicated by wing length. Because size varies with sex and age in the junco, the independent effect of these variables on dominance is difficult to determine; however, size appears to be the best single indicator of status. Early arrival on the wintering grounds also contributes positively to status.

Because males are dominant and dominants are reputed to exhibit greater survivorship, females may have responded over evolutionary time to this set of conditions by migrating south of regions of maximal male abundance in order to lessen the effects of intersexual competition.

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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 contributions 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 statements applicable to the Fuertes Awards also are 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 2 Fuertes Awards have been made, in some years, one amount given is $200.00 per award. One Nice Award is made annually in the amount of $200.00. Interested persons may write to Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. Completed applications must be received by 1 Feb. 1980. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 19–23 March 1980.

NOTICE OF SYMPOSIUM ON NEW HAMPSHIRE ENDANGERED SPECIES

A symposium to recommend vertebrate species for the New Hampshire Fish & Game Department's State List of Endangered Species will be held on 1 December 1979 at the Harris Center for Conservation in Hancock, N.H., co-sponsored by the Audubon Society of New Hampshire, the Harris Center, and the New Hampshire Fish and Game Department. Persons with pertinent information on New Hampshire species of mammals, birds, reptiles, amphibians or fresh water fish that should be considered for endangered or threatened status, should contact Carol Smith, Audubon Society of New Hampshire, 3 Silk Farm Road, Concord, New Hampshire 03301 (603-224-9909) by 15 October.

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PHENETIC RELATIONSHIPS WITHIN THE FAMILY GRUIDAE

D. Scott Wood

The monographs on the Gruidae by Blythe and Tegetmeier (1881) and Blaauw (1897) indicate that the cranes were studied extensively in the 19th century. However, opinions of taxonomists of that time differed widely as to the generic and specific limits within the family. Sharpe (1899) listed 19 species and 9 genera while Blythe and Tegetmeier (1881) and Blaauw (1897) recognized 16 species in 2 and 3 genera, respectively. Little systematic work has been conducted on cranes in the 20th century except to address questions of nomenclature and to describe subspecies (e.g., Peters 1925, Grant 1948, Walkinshaw 1965). Peters (1934) proposed the classification in general use today (4 genera, 14 species) and the only changes in generic or specific limits have concerned *Balearica* (Walkinshaw 1964). Archibald (1975) reevaluated phylogenetic relationships within the Gruidae by examining the structure of the unison calls. He studied 13 of the 15 species (recognizing 2 species of *Balearica*) and recently obtained data on *Grus leucogeranus* (pers. comm.). The classifications of Peters and Archibald are represented in Fig. 1.

Taxonomic investigations and studies dealing with evolutionary patterns or adaptations are particularly reliant on morphologic information. Detailed comparative morphological studies (particularly skeletal) do not exist for the Gruidae and it is my purpose to evaluate the phenetic similarities among the cranes (both external and skeletal) and compare the results with current classifications.

MATERIALS AND METHODS

Up to 10 skins for each of the 15 crane species were measured. Usually the first 10 specimens encountered were measured, but in the few cases where larger series existed (e.g. *Grus canadensis*) I measured equal numbers of males and females. Skeletons of 14 of the 15 species were located. Table 1 details the material used along with the current ranges of the species. The nomenclature is that of Peters (1934) except that 2 species of *Balearica* are recognized in light of Walkinshaw's (1964) work. The original data are contained in appendices to Wood (1976).

I coded 95 external characters (EXT) from each skin including characters from all parts of the body. For coding color characters I used the Munsell system (1973), a numerical scheme which specifies colors using 3 components. Only the component representing the lightness or darkness (gray scale) of the color was used because the remaining components (representing hue and intensity) showed little variation. Measurements of plumage such as lengths of primaries and vane widths of rectrices were made with a rule to the nearest 1.0 mm, and those of other parts with dial calipers to 0.1 mm.

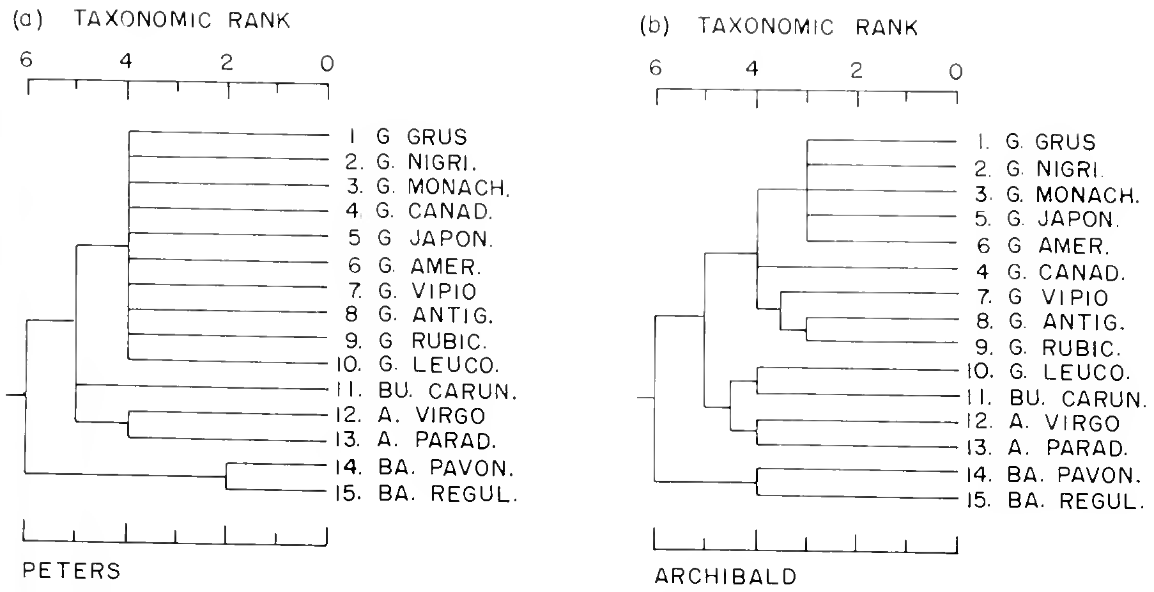

FIG. 1. Dendrograms representing the classifications of cranes proposed by Peters (1934) and Archibald (1975, pers. comm.). Taxonomic levels have been arbitrarily assigned the following values: (2) species, (3) subgenus, (4) genus, (5) subfamily, (6) family.

The head and neck region was divided into 19 areas and each coded for the amount of feathering using a scale of 0 (no feathers) to 5 (fully feathered). I coded 21 two-state (presence or absence) characters to take into account the special features of the various species.

A total of 55 skeletal measurements (SKEL) was taken with either dial or vernier calipers to the nearest 0.1 mm. Characters 1–50 are those of Schnell (1970a) with appropriate modifications due to differently shaped bones in the cranes. Characters 51–55 are designed to measure the tracheal invagination into the sternum. Both external and skeletal characters are described in the appendix of Wood (1976).

Models (based on principal component analyses) and phenograms were constructed using techniques such as those employed by Schnell (1970a,b), Robins and Schnell (1971) and Hellack (1976). Computations were performed on the IBM 370 computer using the computer program package NT-SYS developed by F. J. Rohlf, J. Kishpaugh and D. Kirk. The reader is referred to Schnell (1970a) and Sneath and Sokal (1973) for full details on these methods.

A preliminary principal component analysis was conducted on the data after logarithmic transformation and standardization to evaluate the effect of size. Size has been shown to be a major component of the variation in other phenetic studies on birds (Schnell 1970a, Robins and Schnell 1971, Hellack 1976, Hellack and Schnell 1977). Thus, I followed their suggestions and transformed my data to reduce this effect. Sternum length and humerus length were used as divisors of all skeletal measurements to form 2 transformed data matrices composed of ratios (SKEL/STERNUM, SKEL/HUMERUS). External dimensional measurements were divided by a size factor (sum of wing length, length of bare tibia and tarsus length) and combined with the 2-state characters to form a data set (EXT-WO/COLOR). The color characters were added to these data to form a second data set of external characters (EXT/LENGTHS). SKEL/STERNUM and EXT/LENGTHS were combined to form a data set over all characters (COMBINED).

TABLE 1

NUMBER ASSIGNED TO EACH SPECIES OF CRANE. NUMBER OF SKINS AND SKELETONS MEASURED AND GEOGRAPHIC DISTRIBUTION OF SPECIES[a]

Name[b]	No. skins	No. skeletons	Current distribution (B) Breeding; (W) Wintering; (R) Resident
1. *Grus grus* Common Crane	10	10	(B) Northern Eurasia, India; (W) Mediterranean, India, China
2. *Grus nigricollis* Black-necked Crane	10	0	(R) Tibet, Kashmir, to Viet Nam
3. *Grus monacha* Hooded Crane	9	1	(B) Central Siberia; (W) Japan, S. Korea, S. China
4. *Grus canadensis* Sandhill Crane	10	10	(B) Northern N. Am., southeast U.S.A., Cuba; (W) southern U.S.A., Mexico, Cuba
5. *Grus japonensis* Manchurian Crane	10	8	(B) Eastern Siberia, Manchuria, Japan; (W) Japan, Korea
6. *Grus americana* Whooping Crane	10	10[c]	(B) Wood Buffalo Park, Canada; (W) Aransas Natl. Wildl. Ref., Texas, U.S.A.
7. *Grus vipio* White-naped Crane	9	8[c]	(B) Southeast Siberia, northwest Mongolia; (W) Central China, South Korea
8. *Grus antigone* Sarus Crane	10	10	(R) India, Burma, Malaya, northeast Australia
9. *Grus rubicunda* Brolga	10	7	(R) Western and northern Australia
10. *Grus leucogeranus* Siberian Crane	9	6	(B) Northern Siberia; (W) Asia Minor (?), India, China
11. *Bugeranus carunculatus* Wattled Crane	9	7	(R) East and south Africa
12. *Anthropoides virgo* Demoiselle Crane	10	10	(B) North Africa, southern U.S.S.R. to Mongolia; (W) North Africa to Burma
13. *Anthropoides paradisea* Stanley Crane	8	10	(R) Africa south of the Zambesi River
14. *Balearica pavonina* West African Crowned Crane	10	10	(R) Africa between 0° and 15° N latitude
15. *Balearica regulorum* Gray Crowned Crane	10	10	(R) Africa south of the equator

[a] Distributions taken from Walkinshaw (1973).

[b] Species names from Peters (1934) and Walkinshaw (1964); common names from Walkinshaw (1973).

[c] Includes 2 partial skeletons.

For all data matrices, characters were standardized to a mean of 0 and standard deviation of 1. A matrix of correlations among characters was computed and from it principal components were extracted. The crane species were projected onto the first 3 components and plotted using the computer package GRAFPAC developed by F. J. Rohlf. The shortest minimally connecting network was superimposed on each of the 3-dimensional models to indicate distortion. Character loadings were computed for each of the components to identify the sources of variation; loadings of the first 3 principal components for each analysis are contained in appendices to Wood (1976). The correlation between (1) a matrix of euclidean distances between species in the 3-d model and (2) the corresponding distance matrix (described below) was calculated to give a matrix correlation coefficient. This coefficient gives an indication of how well the 3-d model represents the distance matrix.

Product-moment correlation and average distance coefficients were computed for all pairs of species. Cluster analyses using the unweighted pair-group method with arithmetic averages (UPGMA) were performed on all correlation and distance matrices (basic similarity matrices, abbreviated BSMs) and the results summarized in phenograms. Matrix correlation coefficients were calculated to indicate the degree of concordance between similarity values in a phenogram and its BSM.

To compare the results of this study with the work of other authors, similarity matrices were constructed from the classifications of Peters (1934) and Archibald (1975, pers. comm.). For details of this procedure see Schnell (1970a). These were combined with the BSMs and correlations between all pairs of matrices were computed. The similarity matrix produced was subjected to clustering using UPGMA and the results summarized in a phenogram. The classifications of Peters and Archibald were compared to my phenograms in a similar manner.

The following abbreviations are used. Specific BSMs are named by hyphenating CORR or DIST (depending on the type of similarity coefficient used) to the appropriate data matrix (e.g. CORR-EXT/LENGTHS). Phenograms derived from specific BSMs bear the name of the BSM. The classifications of Peters (1934) and Archibald (1975, pers. comm.) are denoted by PETERS and ARCHIBALD, respectively.

RESULTS

Three-dimensional models.—The ordination of the crane species with respect to the first 3 principal components derived from EXT/LENGTHS is shown in Fig. 2. Components I, II and III explain 28.6, 17.2 and 11.2% of the character variance for a total of 56.9. In spite of the low percentage, the model is an excellent representation of the BSM DIST-EXT/LENGTHS: the matrix correlation being 0.97. Other 3-d models also show a high matrix correlation regardless of how much character variance is explained by the principal components. The *Balearica* species (14, 15) are separated by principal component I (PC-I) which has high (absolute value >0.8) negative loadings on a complex of wing (EXT 32, 36, 38, 40, 42), tarsus (EXT 53) and feathering (EXT 66, 70) characters and high positive loadings on 2 tail (EXT 48, 49) and 4 two-state (EXT 81, 85, 89, 93) characters. Crowned cranes have narrower outer vanes on the primaries, shorter tarsi, longer tails

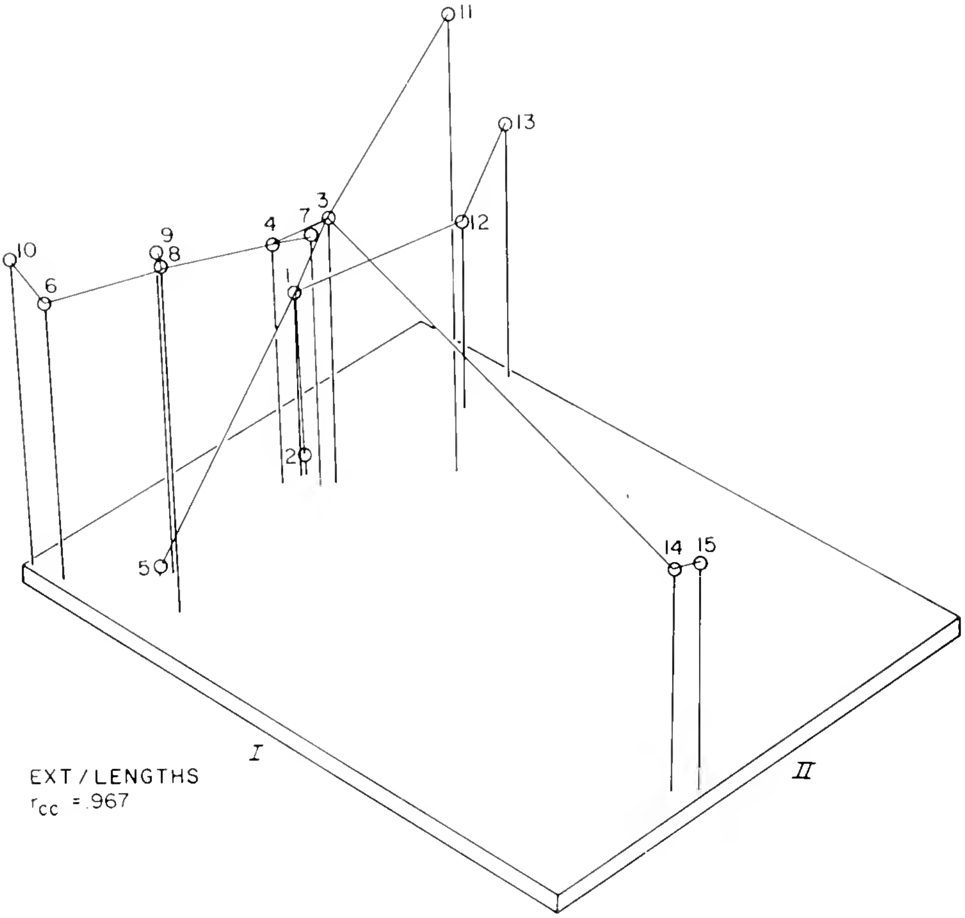

FIG. 2. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among external characters divided by the sum of wing and leg lengths (see text). I and II are indicated and the height represents component III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

and less feathering on the gular and auricular areas than other cranes (all measurements except feathering are relative to the size factor and are ratios). The 2-state characters indicate the presence of special features such as the crest and the oval nostrils.

The remaining cranes are spread along a continuum by PC-II which has high positive loadings (0.7) on characters dealing with lengths of secondaries (EXT 43, 45, 47), color of the outer secondaries (EXT 19) and the width of the mandibular ridge (EXT 29). *Grus americana* (6) and *G. leucogeranus* (10) are whiter than other cranes and larger (relative to the size factor) for the dimensional measurements listed. *Anthropoides* spp. (12, 13) are smaller relative to the size factor and darker than other cranes. PC-III has high positive loadings on the colors of 3 neck regions (EXT 7, 13, 17) and a high negative loading on EXT 80 (a feather contrast). *Bugeranus* (11), *G. japonensis* (5) and *G. nigricollis* (2) are separated from all other cranes

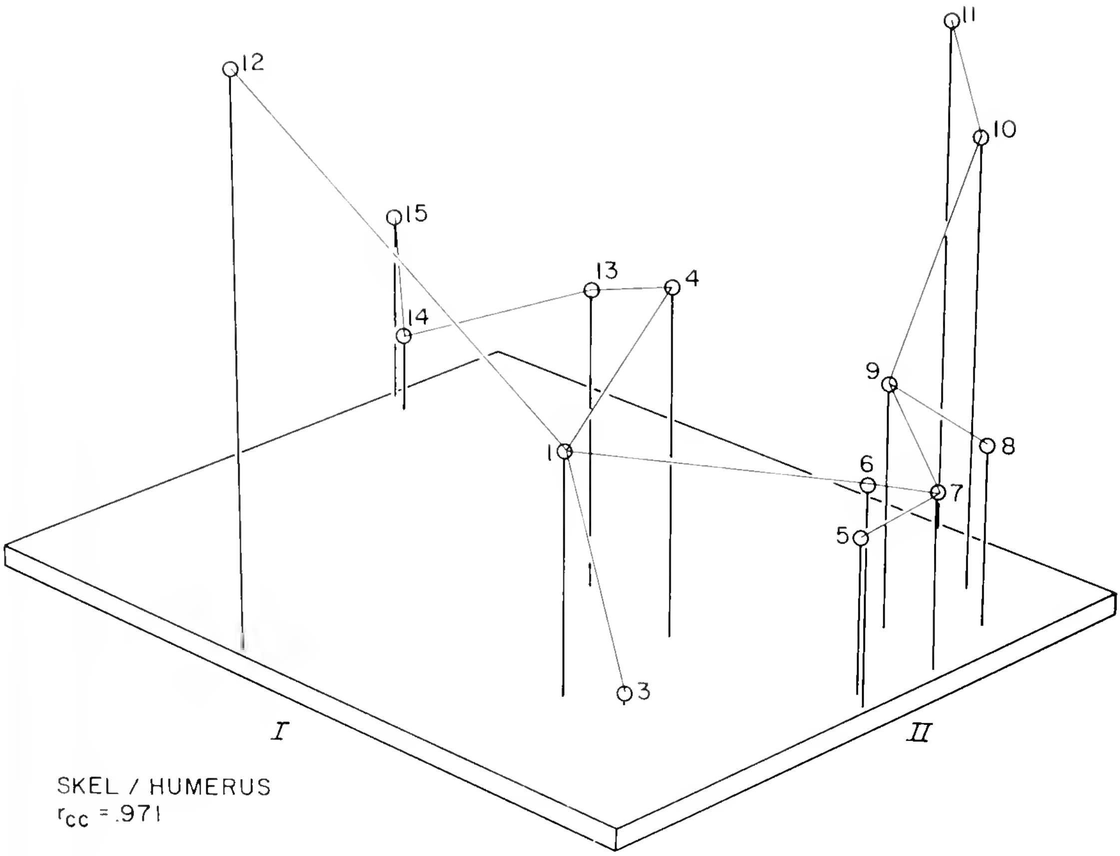

FIG. 3. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among skeletal characters divided by humerus length. Principal components I and II are indicated and the height represents III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

by this component. *Bugeranus* (11) has very light colors for these neck regions and no contrast in the secondary coverts whereas the 2 *Grus* (2, 5) have the opposite condition. The other species are intermediate or exhibit a mixture of these characteristics.

Fig. 3 depicts the 3-d model of SKEL/HUMERUS. *Anthropoides virgo* (12) is separated from the others and among the other species 3 relatively tight groups are present: (A) *G. japonensis*, *G. americana*, *G. vipio*, *G. antigone* and *G. rubicunda* (5–9); (B) *G. leucogeranus* and *Bugeranus* (10, 11); and (C) *Balearica* (14, 15). In the center is a loose aggregation of the remaining *Grus* (*G. grus*, *G. monacha*, *G. canadensis* [1, 3, 4]) and *Anthropoides paradisea* (13). The matrix correlation coefficient is 0.97 and the components explain 37.8, 17.8, and 13.6% of the variance, respectively (total 69.2). PC-I has high positive loadings on several bill and furcular characters (SKEL 1, 2, 11, 12, 13, 19, 20), posterior synsacrum length (SKEL 27) and sternal head width (SKEL 51) and high negative loadings on skull width

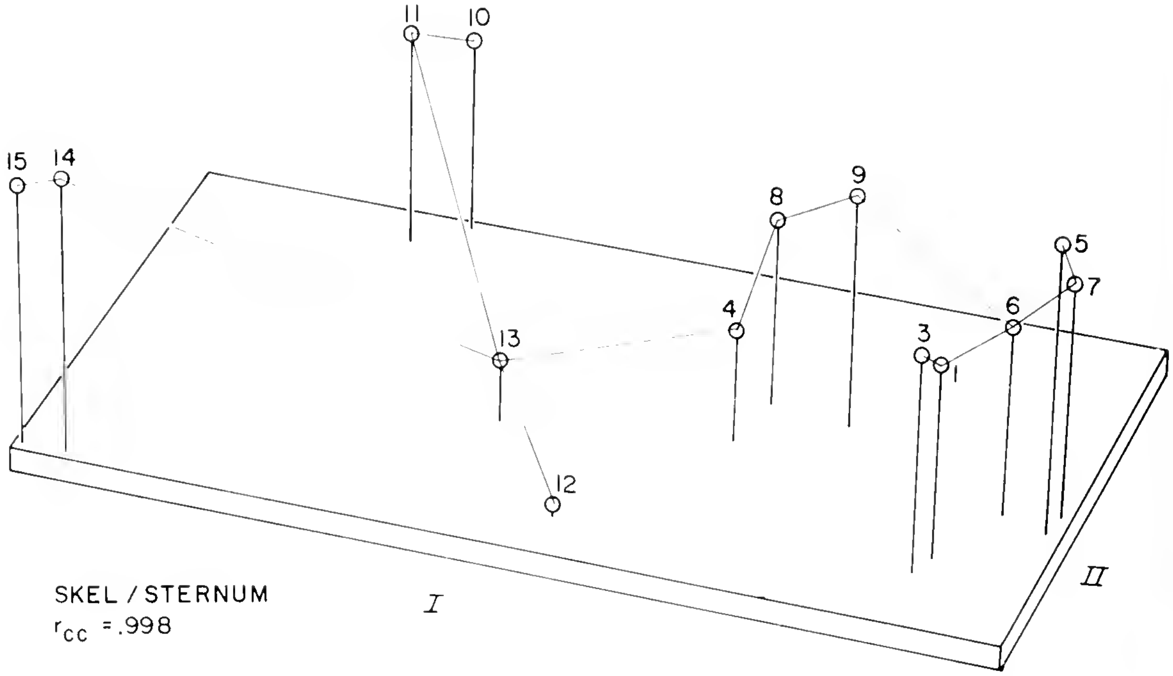

FIG. 4. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among skeletal characters divided by sternum length. Principal components I and II are indicated and the height represents III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

(SKEL 8) and carpometacarpus depth (SKEL 45). The *Balearica* (14, 15) have, relative to humerus length, shorter bills, furculae and synsacra and narrower sternal heads but wider skulls and carpometacarpi than other cranes. PC-II is a contrast of carpometacarpus and phalanx lengths (SKEL 47, 49) and tibiotarsus length (SKEL 36). Relative to humerus length, *A. virgo* (12) has longer hand bones, a shorter tibiotarsus and deeper mandibles than other cranes. Species at the back of the diagram (e.g. *G. leucogeranus* [10] and *Bugeranus* [11]) have the opposite condition. PC-III separated *G. leucogeranus* (10) and *Bugeranus* (11) from the other species as well as further isolating *A. virgo* (12). These species have (relative to humerus length) narrower leg bones than other cranes. This is shown by high negative loadings on characters SKEL 32, 35, and 39.

As in SKEL/HUMERUS, *Balearica* (14, 15) and *G. leucogeranus* and *Bugeranus* (10, 11) form distinct clusters in the 3-d model of SKEL/STERNUM (Fig. 4). *Anthropoides* spp. (12, 13) are found in the center of the model and remaining *Grus* spp. (1–9) are in a loose group (with 2 parts) on the right. The first 3 components explain more than 90% of the variation (71.6, 16.2, 4.7%) and the matrix correlation is 0.998. PC-I has high negative loadings on all but 14 characters and PC-II has high negative loadings on 7 of these 14 (SKEL 1, 2, 4, 11, 12, 13, 20: all from the bill and furcula).

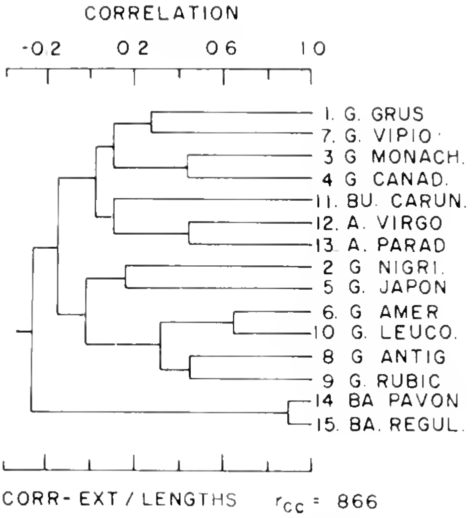

FIG. 5. Correlation phenogram of cranes based on external characters divided by the sum of wing and leg lengths (see text).

Thus, relative to sternum length, the *Balearica* species (14, 15) as well as *Bugeranus* (11) and *G. leucogeranus* (10) are larger than other cranes in all dimensions except bill length, furcula length and keel depth (PC-I). *Bugeranus* (11) and *G. leucogeranus* (10) also have (relative to sternum length) the longest bills and furculae of the cranes whereas *Balearica* (14, 15) have the shortest (PC-II). PC-III has a high negative loading on keel depth (SKEL 23). This means that *Anthropoides* (12, 13) have shallow keels relative to sternum length. PC-I also has high loadings (positive) on SKEL 51–55 (tracheo-sternal characters). Thus, PC-I is a contrast between the sternal invagination by the trachea and most of the rest of the skeleton; the *Balearica* (14, 15) and *Bugeranus* (10, 11) groups show little or no tracheal invagination.

Phenograms.—In the CORR-EXT/LENGTHS phenogram (Fig. 5) there are 3 major clusters: (A) *Balearica*; (B) *Bugeranus*, *Anthropoides*, and 4 *Grus* species (*G. grus*, *G. monacha*, *G. vipio* and *G. canadensis*); and (C) the remaining species of *Grus*. The *Grus* species form species pairs and are separate from *Bugeranus* and *Anthropoides* in group B. The matrix correlation of 0.87 indicates a relatively good fit of the phenogram to its BSM.

Except for 3 species, the clusters using distances (DIST-EXT/LENGTHS; see Fig. 6b in Wood [1976]) are the same as in CORR-EXT/LENGTHS. *G. japonensis* and *Bugeranus* are each quite distant from all other species (shown by component III of Fig. 2) and *G. nigricollis* clusters with *G. grus*, *G. vipio*, *G. monacha* and *G. canadensis*. The matrix correlation of 0.92 indicates a good fit of the BSM.

The 2 phenograms derived from EXT-WO/COLOR (only the distance phenogram is shown; Fig. 6; see Fig. 7a in Wood [1976] for the correlation

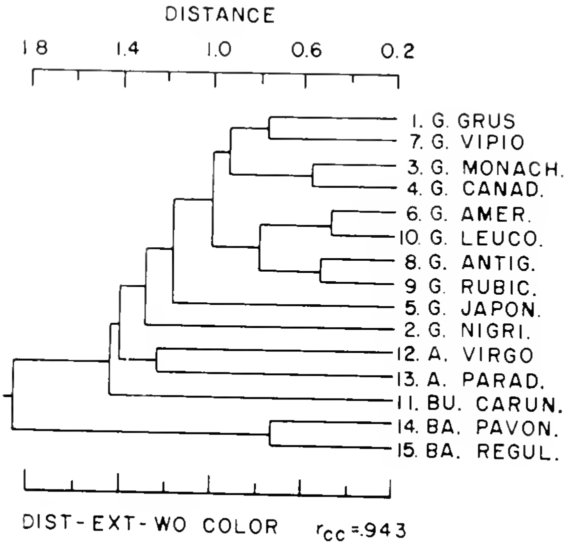

FIG. 6. Distance phenogram of cranes based on external dimensional characters (EXT 28–58) and 2-state characters (EXT 75–95) (dimensional characters divided by the sum of wing and leg lengths).

phenogram) differ from those of EXT/LENGTHS mainly in the placement of the *Anthropoides* species and *Bugeranus*: these species are not associated with any *Grus* species in both CORR- and DIST-EXT-WO/COLOR. As in EXT/LENGTHS, *G. nigricollis* and *G. japonensis* do not cluster consistently with other species: otherwise the *Grus* species show the same split in both analyses. The matrix correlation of 0.94 for DIST-EXT-WO/COLOR is the highest recorded in this study. CORR-EXT-WO/COLOR has a matrix correlation of 0.84 indicating a moderately good fit of the BSM.

CORR-SKEL/HUMERUS (Fig. 7a) is quite different from the external analyses. Two major groups are apparent: (A) *Balearica, Anthropoides, G. grus, G. monacha* and *G. canadensis*; and (B) *Bugeranus* plus the remaining *Grus*. Group A is split into 2 subgroups with *Anthropoides paradisea* and *Balearica* being separated from *Grus* and *A. virgo*. Group B shows a less distinct split and most species are arranged in pairs. Certain species associations are similar to ones found in the external analyses: (1) *G. grus, G. monacha, G. canadensis*; (2) *Balearica*; and (3) *G. antigone, G. rubicunda*. The matrix correlation of 0.77 indicates that the phenogram represents its BSM less well than do others in this study.

DIST-SKEL/HUMERUS (Fig. 7b) is different from both CORR-SKEL/HUMERUS and from the external analyses. *Anthropoides* is split, as in CORR-SKEL/HUMERUS, but *A. paradisea* clusters with *G. grus* and *G. canadensis* while *A. virgo* is relatively distant from all other species. *G. leucogeranus* and *Bugeranus* cluster as in CORR-SKEL/HUMERUS but the arrangement of the other *Grus* species is different from that analysis. The

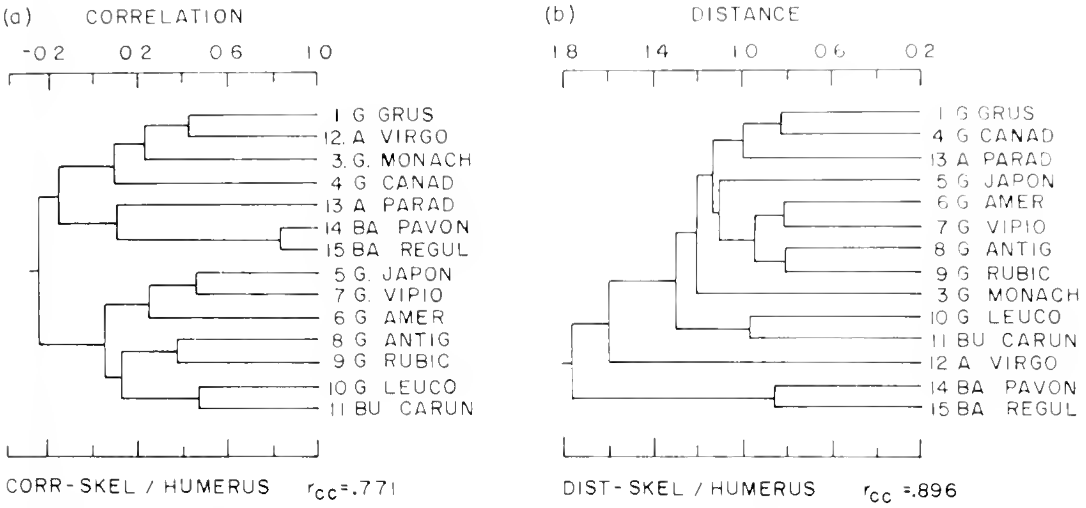

FIG. 7. Correlation (a) and distance (b) phenograms of cranes based on skeletal characters divided by humerus length.

only similarities to the external analyses are the association of *G. americana, G. antigone* and *G. rubicunda* and the separation of *Balearica* from other species. The matrix correlation of 0.90 indicates a good fit to the BSM.

With the exception of *G. leucogeranus*, the major groups of CORR-SKEL/STERNUM (Fig. 8) correspond to the genera recognized by Peters (1934, Fig. 1a). *G. leucogeranus* is very close to *Bugeranus* as in SKEL/HUMERUS. The high matrix correlation of 0.92 indicates a good fit of the BSM.

Like CORR-SKEL/STERNUM, the major clusters of DIST-SKEL/STERNUM (see Fig. 9b of Wood [1976]) correspond closely to the groupings of Peters (1934). *G. leucogeranus* is the only exception, clustering (as in all

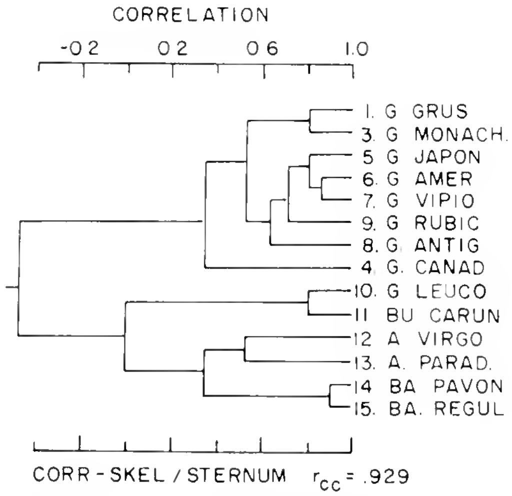

FIG. 8. Correlation phenogram of cranes based on skeletal characters divided by sternum length.

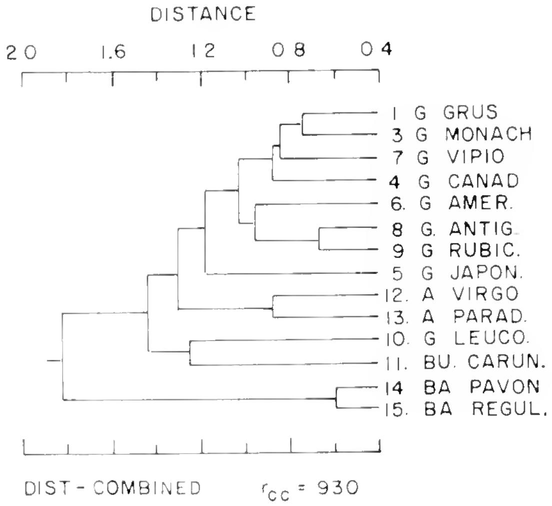

FIG. 9. Distance phenogram of cranes based on external characters divided by the sum of wing and leg lengths and skeletal characters divided by sternum length.

skeletal analyses) with *Bugeranus*. Within *Grus* the species associations are the same as CORR-SKEL/STERNUM except that *G. antigone* and *G. rubicunda* cluster with *G. canadensis*. *Anthropoides* is on the average closer to the *Grus* cluster than to the other species. The matrix correlation of 0.87 indicates a good fit of the BSM.

Two major groups are present in CORR-COMBINED (see Fig. 10a of Wood [1976]): (A) *Anthropoides*, *Balearica* and *Bugeranus*; and (B) *Grus*. Within the first group, *Anthropoides* is separated from *Bugeranus* and *Balearica* and within the second, *G. antigone*, *G. rubicunda* and *G. leucogeranus* are separated from the remaining *Grus*. The arrangement of the *Grus* species is most similar to the external analyses except that *G. americana* clusters with *G. grus* and *G. monacha* in CORR-COMBINED rather than with *G. antigone* and *G. rubicunda*. The matrix correlation of 0.83 is low for this study but still indicates a good fit.

With the exception of *G. leucogeranus*, the clusters in DIST-COMBINED (Fig. 9) correspond to Peters' (1934) genera. This species is most similar to *Bugeranus* (as in the skeletal analyses). *Anthropoides* is closer to *Grus* than to *Bugeranus* and *Balearica* is distant from all other species. The matrix correlation is 0.93.

DISCUSSION

Stability of clusters.—The most stable cluster throughout the analyses is that of the *Balearica* species. In every analysis these 2 species are more similar to each other than either is to another species. *Balearica* is divergent from all other species in 6 of 10 analyses. In the 4 remaining analyses it is always more similar to *Anthropoides* or *Bugeranus* than to *Grus*.

The *Anthropoides* species cluster together in all but SKEL/HUMERUS. This appears to be due to the choice of humerus length as a divisor. Apparently the humerus of *A. virgo* (relative to other bones) has evolved in a manner slightly different from the humeri of other cranes. *Anthropoides* is more often closer to *Grus* species (5 of 8 analyses) than to either *Bugeranus* or *Balearica*.

Grus (excluding *G. leucogeranus*) exists as a major group in all of the analyses except CORR-EXT/LENGTHS, DIST-EXT/LENGTHS and CORR-SKEL/HUMERUS. Within the *Grus* group(s), species are often loosely connected with several species demonstrating no consistent associations. However, several clusters appear relatively constant. *G. antigone* and *G. rubicunda* represent the most stable *Grus* pair appearing in the same cluster in all analyses and as a species pair in all but one (CORR-SKEL/STERNUM). That these 2 species are very similar is further evidenced by their successful hybridization in a recently developed area of sympatry in Australia (J. G. Blackman: quoted by G. W. Archibald, pers. comm.).

Except for SKEL/HUMERUS, *G. grus*, *G. monacha*, and *G. vipio* cluster in the same major group and are often closely associated. Like the *G. antigone-G. rubicunda* pair, these 3 species are sympatric over parts of their ranges and at least 2 (*G. grus* and *G. monacha*) are known to hybridize in the wild (Walkinshaw 1973).

The remaining *Grus* species cluster much less consistently with other species of the genus: *G. nigricollis* is represented only in the external analyses but does not cluster consistently; *G. canadensis* clusters with *G. monacha* in the external analyses but is not consistent elsewhere; *G. americana* clusters with *G. leucogeranus* in the external analyses but is more similar to *G. vipio* in the others; finally, *G. japonensis* forms its own group in more than half of the analyses.

Grus leucogeranus is very similar to *G. americana* in the external analyses but clusters with *Bugeranus* in the skeletal analyses and in DIST-COMBINED. This is a contrast to the phenetic relationships among the other gruid species, for which the external and skeletal analyses produce similar results.

Relationships among classifications.—To give a more detailed analysis of the relationships among similarity matrices and among phenograms, comparisons were made among all pairs of BSMs as well as all pairs of phenograms. Table 2 gives coefficients of correlation for all pairs of BSMs (lower left) and coefficients of cophenetic values for pairs of phenograms (upper right). Fig. 10 summarizes these relationships in the form of dendrograms.

The matrix correlation coefficient of the dendrogram of BSMs is only 0.68,

TABLE 2

COEFFICIENTS OF CORRELATION FOR PAIRS OF BSMs (LOWER LEFT) AND COEFFICIENTS OF COPHENETIC VALUES FOR PAIRS OF PHENOGRAMS (UPPER RIGHT)[a]

	1	2	3	4	5	6	7	8	9	10	11	12
1. ARCHIBALD		.852	.614	.818	.446	.705	.623	.899	.723	.828	.293	.812
2. PETERS	.852		.788	.943	.640	.820	.666	.883	.570	.671	.387	.831
3. CORR-EXT-WO/COLOR	.509	.691		.833	.922	.830	.685	.710	.446	.468	.473	.603
4. DIST-EXT-WO/COLOR	.783	.894	.787		.688	.878	.605	.870	.500	.618	.348	.816
5. CORR-EXT/LENGTHS	.440	.629	.885	.670		.823	.569	.614	.276	.336	.482	.486
6. DIST-EXT/LENGTHS	.744	.844	.760	.903	.722		.521	.877	.338	.575	.382	.730
7. CORR-COMBINED	.655	.658	.766	.632	.776	.683		.606	.712	.615	.392	.448
8. DIST-COMBINED	.850	.832	.659	.821	.640	.891	.815		.626	.847	.332	.836
9. CORR-SKEL/STERNUM	.748	.634	.462	.516	.442	.505	.817	.756		.766	.354	.542
10. DIST-SKEL/STERNUM	.817	.686	.443	.609	.398	.630	.787	.910	.858		.282	.673
11. CORR-SKEL/HUMERUS	.559	.575	.527	.491	.520	.501	.749	.635	.732	.653		.366
12. DIST-SKEL/HUMERUS	.769	.794	.557	.709	.506	.700	.665	.798	.696	.750	.746	

[a] The absolute value of the coefficients are used since similarity for a distance BSM or phenogram is opposite that for a correlation type.

an indication that considerable distortion exists among the main branches of the dendrogram. All distance BSMs cluster together with PETERS and ARCHIBALD but the correlation BSMs are contained in 3 distinct clusters. In contrast to what has generally been found by other workers (e.g., Schnell 1970b, Robins and Schnell 1971, Hellack 1976, Hellack and Schnell 1977)

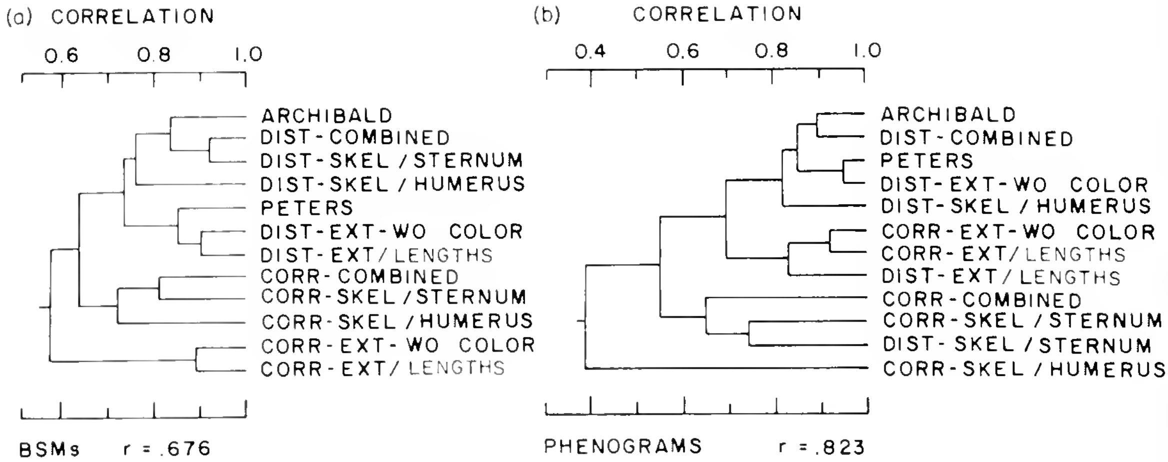

FIG. 10. Dendrograms of cranes showing relationships among basic similarity matrices (BSMs) (a) and phenograms (b). The classifications of Peters (1934) and Archibald (1975, pers. comm.) are included in both dendrograms.

distances give the most uniform results. The average correlation between distance matrices is 0.77 whereas the average between correlation matrices is only 0.67 (see Table 2). Within both the correlation and distance clusters external analyses are grouped together. Skeletal and combined analyses are likewise grouped. There is greater similarity within either the external analyses (mean correlation 0.79) or the group of skeletal and combined analyses (mean correlation 0.76) than between these groups (mean correlation 0.60).

The previous classifications used in this study (PETERS, ARCHIBALD) are each more similar to 1 or more of the BSMs than to each other. This does not reflect a lack of similarity between PETERS and ARCHIBALD but rather demonstrates the close similarities between previous classifications and results of this study. ARCHIBALD is more similar to the skeletal analyses whereas PETERS is more similar to the external analyses. Archibald (1975) based his classification on the unison calls of cranes which directly reflect a portion of the skeletal features (tracheo-sternal), but not the external characters. Peters (1934) apparently relied more heavily on external morphology in constructing his classification.

The relationships among phenograms appear somewhat changed from those among BSMs. The general dichotomy between distance and correlation analyses is apparent but CORR-EXT/LENGTHS, CORR-EXT-WO/COLOR and DIST-SKEL/STERNUM have switched clusters. However, DIST-SKEL/STERNUM and DIST-EXT/LENGTHS are most similar to other distance phenograms (see Table 2). The phenogram of CORR-SKEL/HUMERUS is very divergent from all others and also is a relatively poor representation of its BSM (matrix correlation of 0.77, the lowest of any phenogram).

The relationships discussed for BSMs exist also for the phenograms, although less well defined (i.e. greater similarity exists within either the external group or skeletal plus combined group of phenograms than between these groups; correlations average higher within the skeletal plus combined group than within the correlation group). As found for the BSMs, PETERS and ARCHIBALD are most similar to the distance analyses. PETERS is highly correlated (0.94) to DIST-EXT/LENGTHS and ARCHIBALD is correlated to DIST-COMBINED.

Schnell (1970b) found that phenograms were more similar to previous classifications than were the BSMs. He concluded that species were placed (forced) into hierarchical clusters both in previous classifications as well as phenograms. Robins and Schnell (1971), Hellack (1976) and Hellack and Schnell (1977), however, obtained results at variance with these findings. In the present study, 6 of 10 phenograms are more similar to the previous classifications than are their BSMs (not the same 6 for each classification).

However, in only 4 of the 20 comparisons (20%) are the differences in correlation (correlation of phenogram to classification vs. BSM to classification) greater than 0.051. Data from both Schnell (1970b) and Robins and Schnell (1971) show a much higher percentage of differences greater than 0.055 (54% and 71%, respectively) even though the matrix correlation coefficients of the phenograms to their BSMs are similar to those in the present study. This is further evidence that cranes do fall into relatively well defined clusters and are not "forced" into them by the clustering procedure.

Final considerations.—Close similarity exists between PETERS (the classification of the Gruidae currently accepted by most researchers) and DIST-COMBINED (a good representative phenogram of this study). *Grus leucogeranus* is the only species placed in different major clusters in the 2 classifications. As discussed previously, this species shows phenetic affinities to both *G. americana* (external) and *Bugeranus* (skeletal). Clearly 1 set of similarities is convergent since no evidence exists to link *Bugeranus* with *G. americana* (either phenetically or from other taxonomic studies). Further investigation is needed to evaluate the cladistic relationships of these 3 species.

SUMMARY

Techniques from multivariate statistics were employed to evaluate the phenetic (morphologic) similarities among the cranes (Gruidae). Both external and skeletal characters were analyzed using different data sets constructed by transforming and partitioning the data. The analyses included both principal component analysis and cluster analyses using distance or correlation coefficients. The results were summarized in 3-dimensional diagrams and phenograms. Phenograms as well as similarity matrices were compared and contrasted among themselves and with classifications of other authors. Phenetically the cranes form quite distinct groups; these are similar to the groups found in the classification currently in general use (Peters 1934) with the exception of *Grus leucogeranus*. This species is very similar to *Bugeranus carunculatus*, particularly with regard to skeletal characteristics and the two may in the future be considered congeneric.

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INTERFERENCE COMPETITION AND NICHE SHIFTS IN THE BARK-FORAGING GUILD IN CENTRAL ILLINOIS

Joseph B. Williams and George O. Batzli

During the last few decades competition has received increasing attention as an organizational process for natural communities. Numerous studies of avian communities have elucidated differences between similar species which, presumably, reduce competition and thus permit coexistence (Cody 1974). Important insights into community organization can be obtained by studying guilds that vary in composition both in time and space.

Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Downy Woodpeckers (*Picoides pubescens*), White-breasted Nuthatches (*Sitta carolinensis*), and Brown Creepers (*Certhia familiaris*) all reside in deciduous woodlands of central Illinois and forage over the surface of trees.

Red-headed Woodpeckers are territorial and are dominant over all other members of the guild. They breed most years in central Illinois forests, but periodically migrate in the fall when mast crops are low. Thus, a natural experiment occurs rather frequently; the competitive environment of subordinate guild members includes the aggressive Red-headed Woodpecker during some winters but not others.

Earlier Williams (1975) hypothesized that Red-headed Woodpeckers influence the vertical distribution of Downy Woodpeckers. In this paper we test the hypothesis that Red-headed Woodpeckers constrain subordinate guild members along several niche dimensions and compare the ecological relationships among these species during 1 breeding season (April–August 1974) and 2 non-breeding seasons (September–March 1973–74 and 1974–75).

STUDY AREAS

Hart Memorial Woods, chosen for this investigation, is situated along the Sangamon River near Mahomet, Illinois. It contained 2 distinct areas, a relatively dry upland (9.6 ha) and a wetter floodplain (3.4 ha). A detailed analysis of vegetational composition and vertical structure is presented in Williams (1977). Root et al. (1971) provides a description of seedlings and saplings.

Hart upland, containing 565.3 trees/ha, was dominated by white oak (*Quercus alba*), black oak (*Q. velutina*) and red oak (*Q. rubra*). Understory trees, such as elms (*Ulmus rubra* and *U. americana*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and redbud (*Cercis canadensis*) were dense, but contributed much less basal area. The floodplain area, containing 239.9 trees/ha, was dominated by silver maple (*Acer saccharinum*). Bur oak (*Q. macrocarpa*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*) and standing dead trees were also present. Intermittent openings in the canopy were due to the heavy mortality of American elm from Dutch elm disease 15 years earlier (Root et al. 1971). In both upland and lowland, limbs less than 2.5 cm in diameter were found throughout the canopy, but as expected, the largest limbs were more frequent in the lower height intervals (Williams 1977).

Because acorns are an important winter food source for at least 3 guild members (Red-headed Woodpeckers, Red-bellied Woodpeckers, White-breasted Nuthatches; Bent 1939, 1948), we measured acorn production in each area (results in Williams 1977). Mast production was low in the fall of 1973, and Red-headed Woodpeckers vacated our areas. The next year the acorn crop, especially for white oak, was 100-fold higher with the result that Red-headed Woodpeckers overwintered that year.

METHODS

Each study area was divided into 50-m quadrats during the early fall of 1973 and into 25-m quadrats in early fall of 1974. Individual birds of each species were followed for up to 1 h on several days each month; territories and home ranges were mapped by recording movements and aggressive interactions on a map of the area. We banded and color-marked 5 Red-headed Woodpeckers, 4 Red-bellied Woodpeckers, 4 Downy Woodpeckers, and 2 White-breasted Nuthatches during the course of this study. Since Brown Creepers only overwintered on our study areas, they are not included in the analysis of the breeding season.

Birds were censused by direct observation from 1 September 1973 to 30 March 1975. At first, while making behavioral observations, we estimated densities from the number of birds seen. Beginning in December of 1973 birds were counted by systematically examining each study area once a month.

Habitat use was quantified for 6 dimensions: (1) horizontal space used, (2) activity of bird, (3) tree species occupied, (4) height of bird in tree, (5) condition of substrate (dead or alive), (6) limb diameter. Observations were recorded at 10 sec signals given by an electronic metronome (Wiens et al. 1970). Data were collected an average of 10 days each month. After an individual was located, we timed the bird for no longer than 5 min and located a new bird. This method reduced the sample size somewhat, but it also reduced bias by including observations from as many different birds as possible.

Heights of the birds were recorded in 3-m intervals. To ensure accurate estimates we color-marked strategically located trees at 6 m above the ground. We checked with a forester's height finder (model 43130; Forestry Suppliers, Inc.) if we were uncertain of our estimates. Limb diameters were estimated by using the birds as a reference.

Niche breadths, or the tendency to specialize along a particular resource dimension, were calculated using Levin's (1968) formula. To facilitate comparison of breadth values for resource dimensions with different numbers of resource states, we scaled each value (Fager 1972) so that $B_{max} = 1$ and $B_{min} = 0$.

Interspecific comparisons were tested for significance using original data (number of observations) by Chi-square contingency analysis. Because of the large number of comparisons made, we recognize that some results may be spurious. To alleviate this problem, we discuss only trends significant at $P < 0.01$.

THE BREEDING SEASON

Red-headed Woodpeckers, absent during the winter of 1973–74 because of a mast crop failure, arrived in Hart Woods on 19 April 1974. Observations

TABLE 1

NUMBER OF AGGRESSIVE INTERACTIONS OBSERVED FOR MEMBERS OF THE BARK-FORAGING GUILD DURING 1 BREEDING SEASON (APRIL–AUGUST) AND 2 NON-BREEDING SEASONS (SEPTEMBER–MARCH). FOR INTERSPECIFIC INTERACTIONS VALUES HORIZONTALLY ARE FOR BREEDING SEASON AND VERTICALLY ARE FOR NON-BREEDING SEASON: RH = RED-HEADED WOODPECKER, RB = RED-BELLIED WOODPECKER, DW = DOWNY WOODPECKER, WBN = WHITE-BREASTED NUTHATCH, BC = BROWN CREEPER, S = STARLING

Interspecific

	RH	RB	S	DW
RH	—	9	15	11
RB	24	—	8	1
S	17	1	—	0
DW	83	7	0	—
WBN	11	3	0	8
BC	3	2	0	0

Intraspecific

	Summer		Winter
RH	37	RH	141
RB	3	RB	9
DW	22	DW	29
WBN	1	WBN	1
		BC	17

of early nesting behavior have been reported by Kilham (1977). By the end of May, 7 pairs occupied the lowland and 3, the upland. A pair of Red-bellied Woodpeckers nested in each area but did not overlap with Red-headed Woodpeckers in horizontal space. Two pairs of Downy Woodpeckers nested in the upland, and 2 in the lowland. Territory and home range maps are presented in Williams (1977).

Sixty-three intraspecific aggressive interactions were witnessed during the breeding season; 37 involved Red-headed Woodpeckers and 22 involved Downy Woodpeckers (Table 1). Most aggression between Red-headed Woodpeckers occurred early in the breeding season. Interspecific conflicts consisted mostly of Red-headed Woodpeckers or Red-bellied Woodpeckers defending their nest cavities against Starlings (*Sturnus vulgaris*). When aggression occurred, Red-headed Woodpeckers always supplanted Red-bellied Woodpeckers; in other cases the larger bird always displaced the smaller.

The niche differences quantified for the breeding community are presented in Williams (1977). Here we summarize our findings and discuss data that yielded the most interesting comparisons between the breeding and non-breeding season.

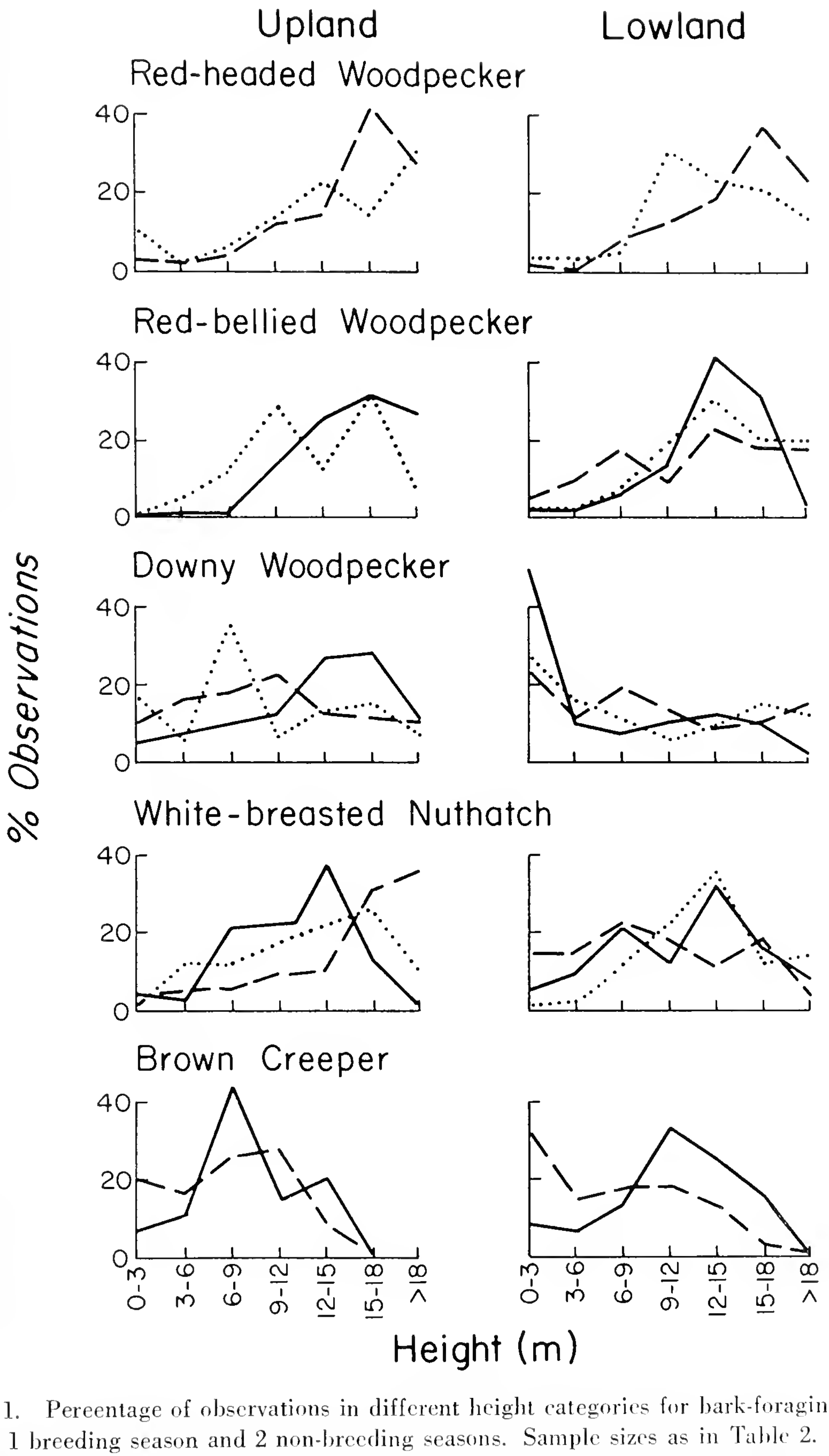

FIG. 1. Percentage of observations in different height categories for bark-foraging birds during 1 breeding season and 2 non-breeding seasons. Sample sizes as in Table 2. Dotted lines represent the breeding season, solid lines represent the 1973–74 non-breeding season, dashed lines represent the 1974–75 non-breeding season.

For the breeding season, Red-headed Woodpeckers foraged by hawking aerial insects and gleaning insects from trees. Red-bellied Woodpeckers procured most of their insect food from the surface of trees. The largest proportion of food obtained by Downy Woodpeckers was by percussion. White-breasted Nuthatches foraged by poking their bills into shallow crevices or gleaning surface insects. In Hart upland Red-headed and Red-bellied woodpeckers principally used white, black, and red oaks as well as dead trees; Downy Woodpeckers exploited understory trees more than other species; and White-breasted Nuthatches favored white oaks. In the lowland, Red-headed Woodpeckers preferred and defended dead trees, and Red-bellied Woodpeckers used mostly maple and oaks. Downy Woodpeckers preferred maple trees but also spent a substantial portion of their time foraging on fallen logs and dead trees. White-breasted Nuthatches were most often observed on oaks.

In both Hart upland and lowland, both *Melanerpes* and White-breasted Nuthatches occupied higher height categories most often, whereas Downy Woodpeckers used the lower portions of the canopy (Fig. 1).

The patterns for use of limbs indicated that Red-headed Woodpeckers, Red-bellied Woodpeckers, and White-breasted Nuthatches each selected medium-sized limbs more often than the extremes (Fig. 2). Downy Woodpeckers tended to forage on small limbs in the lowland.

Niche breadth values were grouped into 3 categories: foraging activities; use of space—the average breadth over horizontal and vertical dimensions; and use of trees—the average breadth for tree species used, amount of dead versus live substrate exploited, and limb diameters employed. For the breeding season, most niche breadth values were intermediate (0.40–0.60) except for those for Red-headed Woodpecker foraging which were consistently low (0.13–0.25; Williams 1977).

THE NON-BREEDING SEASON

From territory maps, home range maps, and census data, we determined that 2 Red-bellied Woodpeckers, 4 Downy Woodpeckers, and 4 White-breasted Nuthatches foraged in the upland and lowland areas of Hart Woods during the 1973–74 winter. Brown Creepers were sporadic in occurrence.

Densities for the 1974–75 non-breeding season were different in both areas. In Hart upland, 19 Red-headed Woodpeckers established winter territories. Red-bellied Woodpeckers sometimes encroached into the upland, but territorial Red-headed Woodpeckers occupied almost the whole upland, and chased Red-bellied Woodpeckers back to the lowland. Four Downy Woodpeckers foraged in the upland and lowland areas. Four White-breasted Nuthatches and 4 Brown Creepers (sporadically) occurred in both the upland and lowland,

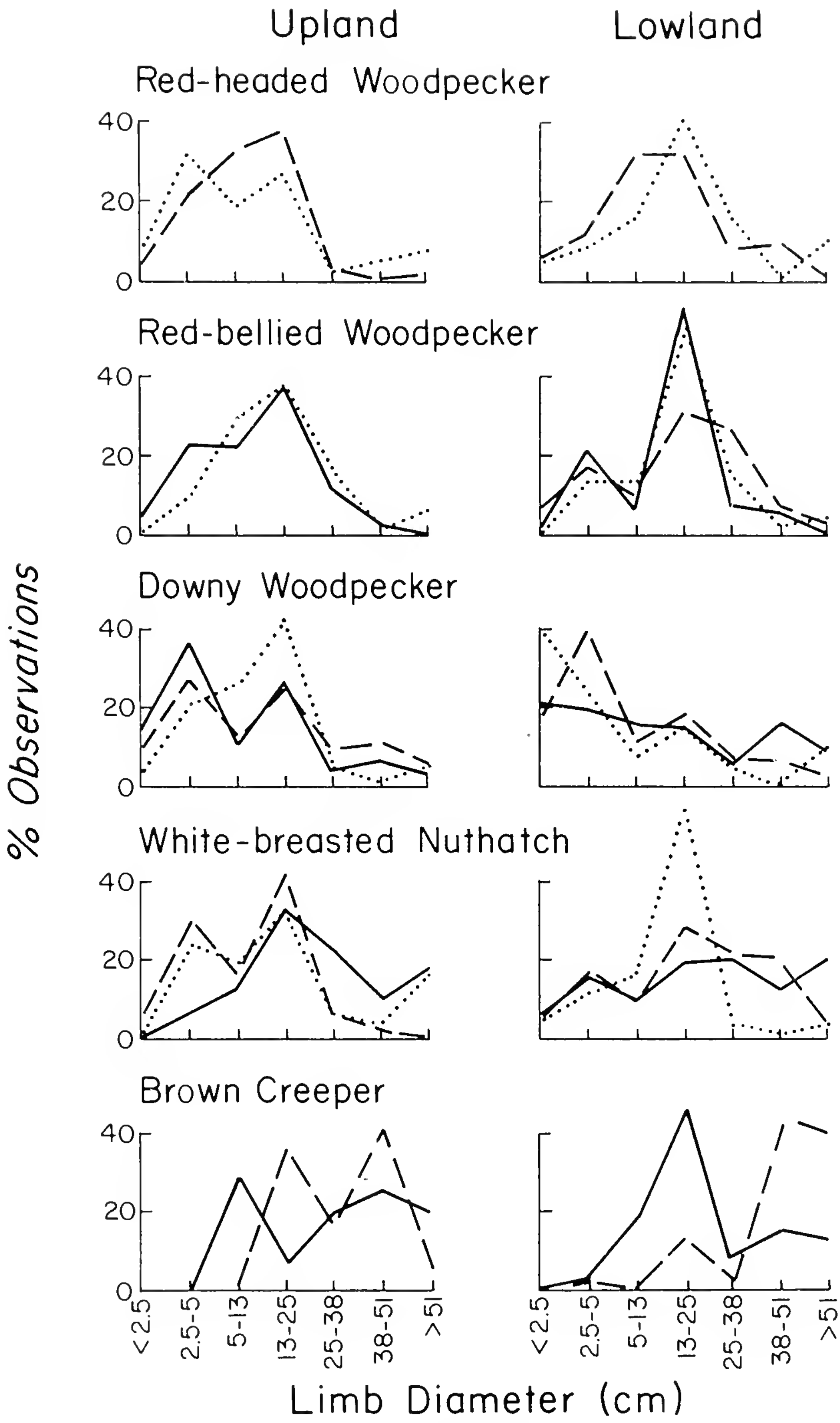

FIG. 2. Percentage of observations on different limb diameters for bark-foraging birds during 1 breeding season and 2 non-breeding seasons. Sample sizes as in Table 2. Dotted lines represent the breeding season, solid lines represent the 1973–74 non-breeding season, dashed lines represent the 1974–75 non-breeding season.

although we found them more often in the lowland. In addition, in the lowland we observed 2 Red-headed Woodpeckers, and 2 Red-bellied Woodpeckers.

Red-headed Woodpeckers attacked conspecifics 141 times during the non-breeding season (Table 1). This value, however, is somewhat misleading in that most of these encounters (99) occurred during September when adults and juveniles established winter territories. Male Downy Woodpeckers often supplanted females but no territorial boundaries were observed. The most numerous interspecific conflicts involved Red-headed vs Downy woodpeckers or Red-headed vs Red-bellied woodpeckers.

The foraging ecology of each species changed during the non-breeding season (Williams 1977). Both *Melanerpes* predominantly used seeds (mostly acorns) whereas during the breeding season insects were their principal food. Downy Woodpeckers foraged by percussing or probing more than any species, just as they did during the breeding season. Searching occupied the major portion of time for White-breasted Nuthatches and Brown Creepers. White-breasted Nuthatches handled seeds more than during the breeding season.

During the 1973–74 season, with Red-headed Woodpeckers absent from the upland, Red-bellied Woodpeckers exploited mostly oaks (Table 2). Downy Woodpeckers, White-breasted Nuthatches, and Brown Creepers also used oaks, but in different proportions for different types. For example, Downy Woodpeckers foraged on white oak more, whereas Brown Creepers preferred black and red oaks. In Hart lowland for the same year, Red-bellied Woodpeckers and White-breasted Nuthatches favored maple and green ash trees, Downy Woodpeckers selected fallen logs most often, and Brown Creepers preferred green ash.

For the 1974–75 non-breeding season, time spent on tree types differed from the preceding year. Having established winter territories on both sites, Red-headed Woodpeckers may have influenced tree selection by other guild members. In the upland Red-headed Woodpeckers and White-breasted Nuthatches preferred white oak, Brown Creepers favored black and red oaks. Downy Woodpeckers also selected white and black oaks, but used understory trees more when Red-headed Woodpeckers were present. In the lowland all 3 woodpecker species selected maple and oaks, whereas White-breasted Nuthatches and Brown Creepers chose maple and green ash most often. The shift of Red-bellied Woodpeckers from ash to oak may have been associated with increased mast production in 1974. Since Red-headed Woodpeckers did not occupy most of the lowland, Red-bellied Woodpeckers had access to the bur oak.

Patterns for foraging height suggested that Red-headed Woodpeckers influenced the vertical distribution of several guild members (Fig. 1). With the absence of Red-headed Woodpeckers (1973–74), Red-bellied and Downy

TABLE 2

TREE SPECIES USED (PERCENT OF OBSERVATIONS) BY BIRDS IN 2 STUDY AREAS DURING WINTER SEASONS

Tree species	Availability index[1] %	Red-headed Woodpecker	Red-bellied Woodpecker		Downy Woodpecker		White-breasted Nuthatch		Brown Creeper	
		74–75	73–74	74–75	73–74	74–75	73–74	74–75	73–74	74–75
				Hart upland						
		(1916)[2]	(422)		(1382)	(963)	(110)	(183)	(62)	(48)
Black oak, red oak	57	40	47	—	23	17	46	16	62	70
White oak	35	51	52	—	66	59	52	79	37	29
Bitternut hickory	2	1	—	—	2	3	—	—	—	—
Elms	2	1	—	—	2	6	1	3	—	—
Logs	1	1	—	—	—	3	—	—	—	—
Other	3	6	1	—	7	12	1	2	1	1
				Hart lowland						
		(580)	(228)	(440)	(641)	(1191)	(152)	(305)	(79)	(190)
Maple	26	38	46	34	24	31	51	45	23	53
Logs	24	—	—	2	36	—	—	—	—	—
Bur oak	13	27	1	18	—	18	5	17	—	3
Green ash	11	1	37	7	6	10	30	19	65	19
Standing dead	7	13	—	1	11	2	13	2	1	13
Hackberry	6	5	—	3	6	3	—	12	—	5
Black walnut	3	—	4	5	1	1	—	1	—	1
Elms	3	—	9	4	3	8	—	—	8	1
Other	8	16	3	26[3]	13	27[4]	1	3	4	7

[1] Based on relative basal area (m^2/ha).
[2] Number of observations in parentheses.
[3] Value includes 8% sycamore (*Platanus occidentalis*) and an array of other oak trees.
[4] Value includes 10% honey locust (*Gleditsia triacanthos*).

woodpeckers and White-breasted Nuthatches used the higher height classes in Hart upland. Brown Creepers foraged below 9 m over 60% of their time. During the same season, lowland data showed that Red-bellied Woodpeckers used the higher height categories, but Downy Woodpeckers foraged in the 0–3 m category 50% of the time, partly because they were using logs.

During the subsequent winter season, height patterns were shifted, especially in the upland where Red-headed Woodpeckers were common. Red-headed Woodpeckers dominated the 12–18 m range, Downy Woodpeckers shifted down to heights less than 12 m almost 50% of the time. White-breasted Nuthatches shifted slightly upward; the Brown Creeper pattern was similar to the preceding year. For the lowland, Red-headed along with Red-bellied woodpeckers again occupied higher zones, Downy Woodpeckers favored the lower zones, White-breasted Nuthatches used height categories more evenly, and Brown Creepers shifted downward.

Both *Melanerpes* occupied the higher height categories during both seasons in both upland and lowland. Downy Woodpeckers consistently foraged low in the canopy in the lowland for both seasons and low in the canopy when Red-headed Woodpeckers were present in the upland.

In the absence of the influence of the dominant competitor (1973–74), Red-bellied Woodpeckers and White-breasted Nuthatches preferred 13.1–25 cm limbs, Downy Woodpeckers chose smaller limbs more often, and Brown Creepers consistently favored trunks and larger branches (Fig. 2). The following winter, Red-headed Woodpecker distributions mimicked Red-bellied Woodpeckers for both areas. White-breasted Nuthatches shifted to smaller limbs in the upland, and Brown Creepers used smaller limbs in both areas. Red-headed and Red-bellied woodpeckers preferred similar limb sizes during breeding and non-breeding seasons, but in the breeding season Downy Woodpeckers employed larger limbs in the upland.

The suggestion of Williams (1975) that Downy Woodpeckers are generalists in winter is supported by our data (Table 3). In most cases, they had the highest niche breadths and Brown Creepers had the lowest. The food habits of Downy Woodpeckers during winter also are the most diverse of all guild members (Williams and Batzli 1979a). Niche breadth for use of total space could not be calculated for 1973–74 because horizontal measurements were inadequate. However. niche breadths for height use generally increased when Red-headed Woodpeckers were present (1974–75) in Hart Memorial Woods. Changes of niche breadths for other dimensions in the presence of Red-headed Woodpeckers were not consistent. Unlike the breeding season, Red-headed Woodpeckers were not the most specialized in foraging activities nor in tree use during the non-breeding season.

In summary, most interspecific aggression between Red-headed Woodpeckers and subordinates occurred during the non-breeding season. Since Red-bellied Woodpeckers ranged over the entire upland during the winter of 1973–74 but foraged only in the lowland during 1974–75, we suggest that Red-headed Woodpeckers constrained Red-bellied Woodpeckers in horizontal space. In the presence of Red-headed Woodpeckers, other subordinate species shifted their use of height, tree species, and limb size. Although each species responded differently, evidence suggested that interference by Red-headed Woodpeckers constrained each subordinate guild member along some niche dimension. Niche breadths for foraging heights of subordinate species generally increased when Red-headed Woodpeckers were present, but responses varied among the species for other dimensions.

TABLE 3

SUMMARY OF NICHE BREADTHS FOR BARK-FORAGING BIRDS DURING 2 NON-BREEDING SEASONS[1]

Species	Foraging activity		Space use			Tree use	
			Height		Total		
	1973–74	1974–75	1973–74	1974–75	1974–75	1973–74	1974–75
			Hart upland				
RH	—	0.43	—	0.42	0.61	—	0.54
RB	0.51	—	0.48	—	—	0.55	—
DW	0.56	0.44	0.69	0.92	0.65	0.55	0.60
WBN	0.34	0.12	0.49	0.50	0.29	0.33	0.29
BC	0.09	0.15	0.43	0.58	0.31	0.47	0.17
			Hart lowland				
RH	—	0.41	—	0.51	0.46	—	0.60
RB	0.16	0.59	0.39	0.83	0.63	0.47	0.48
DW	0.55	0.50	0.37	0.86	0.73	0.70	0.53
WBN	0.34	0.23	0.67	0.81	0.56	0.60	0.46
BC	0.09	0.19	0.52	0.62	0.46	0.19	0.27

[1] Symbols as in Table 1.

DISCUSSION

Most evidence of competitive exclusion in nature is indirect (Orians and Collier 1963). Bock (1970) suggested that, although not a requisite for competition (2 species may exploit a common resource without any physical interaction), overt aggressiveness between 2 species indicates that competition is occurring. In this study, Red-headed Woodpeckers displaced Red-bellied and Downy woodpeckers during both seasons and White-breasted Nuthatches and Brown Creepers during the non-breeding season suggesting that these species compete for resources.

Bock (op. cit.) further reasoned that if direct conflict over a food source (or any resource) is evidence of competition for that commodity, then the frequency and intensity of aggressive encounters should be a quantitative measure of the intensity of that competition. Because the highest number of interspecific aggressive interactions occurred during the non-breeding season and because all members of the bark-foraging guild used acorns as a food source in winter (Williams and Batzli 1979a), we suggest this to be a period of competition among guild members. Most intraspecific encounters for Red-headed Woodpeckers occurred during the early breeding season or early fall when birds established winter territories. These 2 periods may be the most intense period of competition within this species.

Red-bellied Woodpeckers, which occupied upland habitats when Red-headed Woodpeckers were absent, were expelled by Red-headed Woodpeckers the following winter and were forced to forage in areas where fewer oaks occurred, an observation consistent with our hypothesis that the use of space by the guild is strongly influenced by the Red-headed Woodpecker. Other members of the guild, though excluded less intensively from the territories of Red-headed Woodpeckers, still appear to be influenced by them. Downy Woodpeckers shifted to lower foraging sites in the presence of Red-headed Woodpeckers, and they used a larger array of tree species and height categories more evenly in order to acquire sufficient food. Experimental removal of Red-headed Woodpeckers from a nearby woods produced results consistent with those from the natural experiment reported in this paper (Williams and Batzli 1979b).

The "jack-of-all-trades-master-of-none" principle (MacArthur 1972) implies that species should specialize along niche dimensions which increase net gain, thereby increasing competitive ability. If a dominance hierarchy exists, 2 alternatives seem feasible for subordinate species with respect to niche breadth and coexistence. First, as predicted by Morse (1974), subordinates can decrease their niche breadth (or specialize) and exploit only those resources which they use efficiently. Alternatively, a species could increase its niche breadth (or generalize) in order to acquire sufficient resources for maintenance. Downy Woodpeckers increased their breadth along some dimensions when Red-headed Woodpeckers were present.

Downy Woodpeckers did not shift their vertical foraging pattern in the lowland in response to the 2 Red-headed Woodpeckers that established winter territories there. In all cases they foraged low in the canopy where presumably food supplies were higher. Thus, the position of the Downy Woodpecker along the vertical dimension is a function of at least 2 variables, food availability and competitive environment.

SUMMARY

Red-headed Woodpeckers influenced the horizontal distribution of Red-bellied Woodpeckers by aggressively displacing them to the lowland area in winter. In the presence of Red-headed Woodpeckers in the upland, Downy Woodpeckers shifted to lower portions of the canopy and used a wider variety of tree species and limb diameters to acquire food. In the lowland where Red-headed Woodpeckers were less abundant, Downy Woodpeckers did not shift height of foraging regardless of the competitive environment. White-breasted Nuthatches and Brown Creepers also shifted along some dimensions in response to the presence of Red-headed Woodpeckers. During the breeding season interspecific interactions had less influence on foraging patterns of the guild.

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VARIATION IN SUMMER DIET OF GLAUCOUS-WINGED GULLS IN THE WESTERN ALEUTIAN ISLANDS: AN ECOLOGICAL INTERPRETATION

John L. Trapp

The Glaucous-winged Gull (*Larus glaucescens*), like other gulls, is an omnivorous opportunist. Although the literature contains numerous brief references to feeding habits, including discussions of feeding behavior (Moyle 1966) and selective predation (Mossman 1958) at Alaska salmon streams, no detailed analysis of diet has been published. I report here on 2319 regurgitated pellets examined at 4 locations in the western Aleutian Islands, Alaska.

Previous investigations of gull food habits, based wholly or in part on pellet analyses, have been published by Harris (1965), Haycock and Threlfall (1975), Meijering (1954), Otterlind (1948), Threlfall (1968), and Vermeer (1973). Regurgitated pellets probably contain a disproportionate number of certain prey remains. Items such as soft-bodied invertebrates and small fish may not be present in pellets in relation to their occurrence in the diet (Harris 1965). Therefore, the pellets examined in this study do not represent a random sample of food consumed, but merely a sample of prey taken by those gulls eating foods resulting in a pellet.

METHODS

Pellets were examined in the field at the following locations and times: Alaid-Nizki Island—May–July 1976; Agattu Island—August 1974, May–June 1975, June–July 1976; Buldir Island—June and August 1974, June–July and September 1975, July–August 1976; Little Kiska Island—July 1976. No other large gull occurs regularly in the western Aleutian Islands during summer, so pellets were easily recognized as belonging to this species. Most occurred along beaches, in the vicinity of breeding colonies, or in "loafing" areas. All pellet data are lumped by locality in Table 1. A detailed monthly tabulation of the data is available from the author.

Pellet analyses were supplemented by direct observations of feeding gulls. Observational data are discussed in the text whenever they clarify, contradict, or supplement the pellet data.

RESULTS

Glaucous-winged Gulls fed on a large variety of organisms, and species occurrence in pellets varied among islands (Table 1). Pellets examined at Alaid-Nizki and Agattu frequently contained the remains of more than 1 prey species (average of 1.3 and 1.4, respectively). Pellets from the other

TABLE 1

PERCENT OCCURRENCE OF FOOD ITEMS IN REGURGITATED PELLETS OF THE GLAUCOUS-WINGED GULL AT SEVERAL LOCATIONS IN THE WESTERN ALEUTIAN ISLANDS, 1974–76

	Island				
Food item	Alaid-Nitzki (N = 875)	Agattu (N = 738)	Buldir (N = 655)	Little Kiska (N = 51)	Semisopochnoi[1] (N = 137)
Invertebrates (total)	(87.1)[2]	(91.0)	(1.9)	(0.0)	(8.0)
Sea urchin (*Strongylocentrotus polyacanthus*)	80.1	78.9	1.1	—	5.8
Unidentified barnacles (*Balanus* spp.)	5.8	4.9	—	—	—
Unidentified crabs (Decapoda)	0.6	1.5	—	—	—
Chiton (*Katharina tunicata*)	8.0	8.8	—	—	—
Limpets (*Acmaea* spp.)	1.9	3.4	—	—	2.2
Periwinkles (*Littorhina* spp.)	1.5	1.0	—	—	—
Blue mussel (*Mytilus edulis*)	2.5	4.9	—	—	—
Unidentified bivalves (Pelecypoda)	0.5	1.2	—	—	—
Unidentified "kelp fly" (Diptera)	—	—	0.8	—	—
Fish (total)	(0.2)	(2.8)	(19.5)	(76.5)	(5.1)
Birds (total)	(0.2)	(2.8)	(79.2)	(25.6)	(86.9)
Leach's Storm-Petrel (*Oceanodroma leuchorhoa*)	0.1	0.4	20.0	—	—
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	0.1	—	40.0	2.0	2.2
Unidentified storm-petrels (*Oceanodroma* spp.)	—	—	0.8	—	—
Red-faced Cormorant (*Phalacrocorax urile*)	—	0.7	—	—	—
Unidentified cormorants (*Phalacrocorax* spp.)	—	—	—	2.0	—
Black-legged Kittiwake (*Rissa tridactyla*)	—	—	0.2	—	—
Ancient Murrelet (*Synthliboramphus antiquus*)	—	—	10.1	19.6	—
Crested Auklet (*Aethia cristatella*)	—	—	2.9	—	—
Least Auklet (*Aethia pusilla*)	—	—	1.4	—	84.7
Cassin's Auklet (*Ptychoramphus aleuticus*)	—	—	0.2	—	—
Unidentified auklet (*Aethia* spp.)	—	—	1.4	—	—
Tufted Puffin (*Lunda cirrhata*)	—	—	0.2	—	—
Unidentified small bird	—	0.7	0.3	—	—
Unidentified bird feathers	0.2	0.6	—	—	—
Unidentified bird eggs	—	1.1	1.7	2.0	—
Vegetation (total)	(1.8)	(3.4)	(2.0)	(0.0)	(0.0)

TABLE 1 (CONTINUED)

	Island				
Food item	Alaid-Nitzki (N = 875)	Agattu (N = 738)	Buldir (N = 655)	Little Kiska (N = 51)	Semisopochnoi[1] (N = 137)
Crowberry (*Empetrum nigrum*) berries	1.7	1.8	1.5	—	—
Unidentified marine algae	0.2	2.4	—	—	—
Unidentified vegetation	—	1.0	0.5	—	—
Miscellaneous (total)	(17.6)	(23.2)	(4.3)	(0.0)	(0.0)
Beach pebbles	14.1	22.6	0.8	—	—
Steller's sea lion (*Eumetopias jubata*) excreta	6.6	0.7	—	—	—
Steller's sea lion hair	—	0.1	3.5	—	—
Calcareous algae	0.8	1.5	—	—	—
Wood chips	—	0.5	—	—	—
Miscellaneous detritus	—	0.2	—	—	—
Arctic fox (*Alopex lagopus*) hair	—	0.1	—	—	—
Unidentified skin	—	0.1	—	—	—
Paper	0.1	—	—	—	—
Blue glass	0.1	—	—	—	—
Aluminum foil	0.1	—	—	—	—

[1] Data taken from Murie (1959:169).

[2] All values represent percent occurrence in total sample. Values in parentheses are composite totals for invertebrates, fish, birds, and miscellaneous. Summation of columns exceeds 100% in most cases because of overlap (i.e. occurrence of more than 1 prey species per pellet).

islands rarely contained more than 1 prey species (average of 1.1 at Buldir, and 1.0 at both Little Kiska and Semisopochnoi).

Invertebrates.—The sea urchin (*Strongylocentrotus polyacanthus*) was by far the most common invertebrate in the diet, occurring in more than 78% of the pellets from Agattu and Alaid-Nizki (Table 1). Sea urchins are taken from the sublittoral fringe at low tide. Large individuals are dropped from the air onto a hard surface to crack the shell; smaller individuals are swallowed whole (cf. Barash et al. 1975). Chitons (*Katharina tunicata*), barnacles (*Balanus* spp.), blue mussels (*Mytilus edulis*), and limpets (*Acmaea* spp.) were also used as food to some degree on these 2 islands.

An unidentified "kelp fly" (Diptera) was important in the diet at Buldir for a short time in August (Table 1). These flies were extremely abundant in decomposing kelp scattered along the beach, and among offal of the Steller's sea lion (*Eumetopias jubata*). Adult gulls were observed capturing flies by "flycatching." They sat passively on the beach and snapped at passing flies with their bills. Flies were present throughout the summer, but only in late summer did they become numerous enough for gulls to feed on them.

Fish.—No attempt was made to identify fish remains in pellets. In the Aleutian Islands, Glaucous-winged Gulls are known to feed on Pacific herring (*Clupea harengus*), Pacific sandlance (*Ammodytes hexapterus*), and rock greenling (*Hexagrammos lagocephalus*) (pers. obs.). Fish were particularly frequent at Little Kiska and Buldir, where they occurred in 76% and 20% of the pellets, respectively (Table 1). At Buldir, fish comprised an important part of the diet of young gulls; 33% of the pellets examined in nesting colonies (N = 106) contained fish. Nesting colonies were littered with partially digested fish remains, and when handling young gulls they frequently regurgitated fish. On several occasions adult gulls were observed harassing Horned (*Fratercula corniculata*) and Tufted (*Lunda cirrhata*) puffins in an effort to steal fish.

Birds.—Nine species of birds were found in gull pellets (Table 1). Birds were most frequently taken at Semisopochnoi and Buldir, occurring in 87% and 79% of the pellets, respectively. Pellets collected at Semisopochnoi by Murie (1959) indicated that gulls there fed largely on Least Auklets (*Aethia pusilla*). The Least Auklet colony at Semisopochnoi is one of the largest in the Aleutian Islands (Murie 1959:198). At least 8 species were represented in pellets at Buldir, with 3 species (Leach's Storm-Petrel [*Oceanodroma leucorhoa*]; Fork-tailed Storm-Petrel [*O. furcata*]; Ancient Murrelet [*Synthliboramphus antiquus*]) accounting for 89% of the individuals taken.

Storm-petrels were frequent prey at Buldir, where they were found in 61% of the pellets. The method used to capture nocturnal storm-petrels is not known, although they are presumably taken at dusk as they emerge from their burrows. Glaucous-winged Gulls were frequently heard calling, and observed "swarming," shortly after dusk and it was assumed that they were preying on storm-petrels. G. V. Byrd (pers. comm.) has observed Glaucous-winged Gulls methodically inspecting the entrances of storm-peirel burrows for chicks or adults.

Although not reflected in pellet remains, eggs and young of the Red-faced Cormorant (*Phalacrocorax urile*) were preyed on extensively in May and June at Agattu. On many occasions gulls were noted harassing adult cormorants by swooping repeatedly over nests. If an adult was successfully dislodged by these tactics the gull immediately landed on the nest and devoured any eggs or young present. Murie (1959:59) also noted heavy predation on the eggs of this species.

Predation on eggs and young of other cliff-nesting birds, such as Black-legged Kittiwakes (*Rissa tridactyla*) and murres (*Uria* spp.) was probably also underestimated. Gulls were not observed taking kittiwake eggs at Agattu or Buldir, but on several occasions were noted attacking chicks at Agattu. Predation on murre eggs was not observed, but they are probably taken whenever given the opportunity. At Bogoslof Island, in the eastern Aleutians, murre eggs and young are one of the main food sources (Murie 1959:183–184; G. V. Byrd, pers. comm.).

Nocturnal, burrow-nesting Ancient Murrelets breed in large numbers at Buldir, and hatching occurs over an approximately 2-week period in mid-July. During the nightly mass migrations to the sea, chicks and adults are extremely vulnerable to gull predation. The opportunistic gulls made heavy use of this temporarily abundant food source; 46% of 102 pellets examined along North Bight Beach (the main terminous of the nightly exodus) in mid-July contained murrelet remains. Overall, murrelets ranked third in frequency of occurrence in pellets at Buldir. At Little Kiska, a locality at which breeding has not yet been confirmed, murrelets were second in frequency of occurrence.

The frequency of small auklets (*Aethia* spp.) in the diet at Buldir is probably underestimated because few pellets were examined in their talus-slope nesting colonies. Auklets were found in less than 6% of all pellets examined (Table 1), but occurred in 42% of the pellets (N = 73) from nesting colonies. Numerous auklet carcasses were observed on all visits to the colonies. Some were no doubt taken by Peregrine Falcons (*Falco peregrinus*) but the majority probably represented gull predation. It may be significant that of the 11 species of alcids nesting at Buldir, the Crested Auklet (*A. cristatella*) was the largest species found regularly in gull pellets. Pigeon Guillemots (*Cepphus columbus*), Parakeet Auklets (*Cyclorrhynchus psittacula*). Horned Puffins, and Tufted Puffins nested in large numbers but may be too large for gulls to take. On 1 occasion a Glaucous-winged Gull was observed to carry a Tufted Puffin in its bill for about 10 m before dropping it (D. G. Kelleyhouse, pers. comm.).

Vegetation.—Crowberry (*Empetrum nigrum*) berries were taken in late summer at Alaid-Nizki, Agattu and Buldir (Table 1). These berries become ripe in mid-August and were frequently found in pellets examined in the uplands. Marine algae and other unidentified vegetation occasionally found in pellets were probably ingested incidentally.

Miscellaneous.—Small beach pebbles were found in 23% of the pellets from Agattu, 14% of those from Alaid-Nizki, and 1% of those from Buldir (Table 1). These pebbles were probably ingested incidentally by gulls feeding on Steller's sea lion excreta. At Alaid-Nizki large concentrations of sea lions are found on the western half of the island, but none occur on the eastern half; 87% of all Alaid-Nizki pellets with pebbles were found on the western half, compared with 42% of the total sample of pellets. Similarly, nearly all pellets containing pebbles examined on Agattu occurred in the immediate vicinity of sea lion colonies. Occasionally other food items, including sea

TABLE 2

RELATIONSHIP BETWEEN ISLAND PHYSIOGRAPHY, SEA OTTER POPULATIONS, AVAILABLE FOOD RESOURCES, AND THE PRIMARY DIET OF GLAUCOUS-WINGED GULLS

	Island				
	Alaid-Nizki	Agattu	Buldir	Little Kiska	Semisopochnoi
Intertidal zone	Extensive	Extensive	None	Extensive	Moderate
Kelp beds	Moderate	Moderate	Limited	Extensive	Moderate
Sea otter population	Very low	Low	Moderate	High	High
Nesting seabirds	Cormorants Gulls Kittiwakes	Cormorants Gulls Kittiwakes Murres	Petrels Cormorants Gulls Kittiwakes Murres Auklets Puffins	Cormorants Gulls Murrelets	Petrels Cormorants Gulls Auklets
Primary diet	Invertebrates	Invertebrates	Birds	Fish	Birds

lion excreta, were found mixed with pebbles, but in most cases pebbles were the sole component of the pellet. Gulls were observed feeding on sea lion afterbirths during June and July at Agattu and Buldir. They also scavenged the rotting carcasses of both young and adult sea lions throughout the summer.

DISCUSSION

Inter-island differences in diet.—At Alaid-Nizki and Agattu, Glaucous-winged Gulls fed primarily on intertidal invertebrates (87% and 91%, respectively); at Buldir and Semisopochnoi the principal food was birds (79% and 87%, respectively); while at Little Kiska the primary prey was fish (76%). These dietary differences seem largely related to island physiography and the available food source (Table 2).

Alaid-Nizki and Agattu both have extensive intertidal zones, with numerous reefs and offshore rocks. Sea urchins and other marine invertebrates are abundant while the sea otter (*Enhydra lutris*), a major predator on sea urchins (Kenyon 1969:105–132), is either absent or present in small numbers. Buldir and Semisopochnoi both support immense numbers of colonial nesting seabirds, which are easy prey for gulls (storm-petrels and Crested Auklets at Buldir; Least Auklets at Semisopochnoi). Buldir has no intertidal zone and a moderate sea otter population. Marine invertebrates and fish may be taken at Semisopochnoi more frequently than the data suggest. Little Kiska has a very large sea otter population and an extensive intertidal zone. Dense kelp beds surrounding the island provide excellent cover and protection for fish.

Inter-species relationships.—Estes and Palmisano (1974) studied the interrelationship among sea otters, sea urchins, and benthic macrophytes in the Aleutian Islands. They found that littoral and sublittoral community structure varied greatly between islands with and without sea otters. They suggested these differences were principally related to the ecological consequences of sea otter predation. Islands without sea otters had dense invertebrate populations (urchins, mussels, limpets, barnacles) in the littoral and shallow sublittoral zones. These invertebrates were small and sparse on islands with high density sea otter populations, and in their place was a rich assemblage of marine macroalgae.

The results of this study indicate that sea otters may also profoundly affect the diet of Glaucous-winged Gulls. This is most graphically illustrated by comparing the diets among Alaid-Nizki, Agattu, and Little Kiska. All 3 islands have extensive intertidal zones and similar densities of nesting sea birds (Table 2). They differ only in the size of the sea otter population—Little Kiska has a high population (apparently near carrying capacity); Alaid-Nizki and Agattu have low populations. Invertebrates (primarily sea urchins) comprised over 81% of the diet at both Alaid-Nizki and Agattu but were not even represented in the sample from Little Kiska. This suggests that sea otter predation on sea urchins at Little Kiska has made it energetically unfeasible for Glaucous-winged Gulls to exploit this resource.

Fish, an important dietary item at Little Kiska, would benefit from the increased standing crop of macrophytic algae following reduction of the herbivorous sea urchins. Recent work at Attu Island (C. A. Simenstad and J. A. Estes, unpubl.) has confirmed the relationship between the presence of algae (mainly *Alaria fistulosa*, *Laminaria* spp., and *Agarum cribrosum*) and abundance of certain nearshore fishes. However, the relationship is complex and only some species (i.e., rock greenling; sculpin [*Hemilepidotus hemilepidotus*] and others; rock fish [*Sebastes* spp.]) are affected; others (such as offshore or inshore transients) are not. Such species as Pacific herring and Pacific sandlance (both of which are taken by gulls) probably are less affected by kelp abundance than other species.

SUMMARY

More than 2300 regurgitated pellets were examined for prey remains at 4 locations in the western Aleutian Islands. These and direct observation of foraging activities demonstrated that Glaucous-winged Gulls fed on a large variety of organisms, but at any given locality they specialized on those species which were most abundant and vulnerable. Inter-island differences in diet seem related to island physiography, the available food source, and the effects of sea otters on the structure of the nearshore community.

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TIMING OF PRIMARY MOLT AND EGG-LAYING IN GLAUCOUS-WINGED GULLS

Nicolaas A. M. Verbeek

In a study of the timing of molt in relation to the breeding cycle of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*) on Walney Island (54° 05′ N, 3° 15′ W), Lancashire, England, I found that primary molt began toward the end of the incubation period (Verbeek 1977). Johnston (1961) found that Glaucous Gulls (*L. hyperboreus*) in Alaska began to molt their primaries before or at the time of egg-laying. He suggested that molt in this species overlapped with egg-laying so that both could occur at that time when food was most plentiful. If latitude (i.e. the shortness of the summer and/or photoperiod) is an important factor influencing the timing of molt in gulls, one would expect Glaucous-winged Gulls (*L. glaucescens*) on Mandarte Island (48° 38′ N, 123° 17′ W), Georgia Strait, British Columbia, to time their primary molt and egg-laying similarly as do the Herring Gulls on Walney Island.

METHODS

The colony on Mandarte Island was searched carefully each day during the egg-laying period in 1976 and 1977. When I found a nest containing its first egg, I placed a numbered stake at the nest to avoid recording the same nest twice. If I suspected that an egg was the first in a second clutch, following disturbance of the first clutch, it was recorded but ignored in the analysis.

Adult gulls were caught in chickenwire traps placed over the nest once they contained 1 or more eggs. Each gull was examined for the state of molt of its primaries and a record was kept on which nest it was caught. Each primary was scored from 0 (old feather) to 5 (full-grown new feather), depending on its stage of development. The scoring scheme was as follows: old feather (0), dropped or pin feather (1), brush to ⅓ grown (2), ⅓ to ⅔ grown (3), ⅔ to almost full grown (4), and fully grown new feather (5). The primaries of only 1 wing of each bird were scored; the vestigial 11th primary was ignored. If all primaries of 1 wing were new the total score would be 50. Because the gulls could not be caught in the traps after their eggs had hatched I did not capture any gulls whose primaries were all new. The captured gulls could not be sexed accurately in most cases, thus, data presented here ignore possible differences in initiation of primary molt between the sexes.

RESULTS

First eggs were laid in mid-May (Fig. 1). The mean and median date of laying was 28 May in 1976, and 5 June in 1977. The difference between these means is significant ($t = -2.21$, $P < 0.05$).

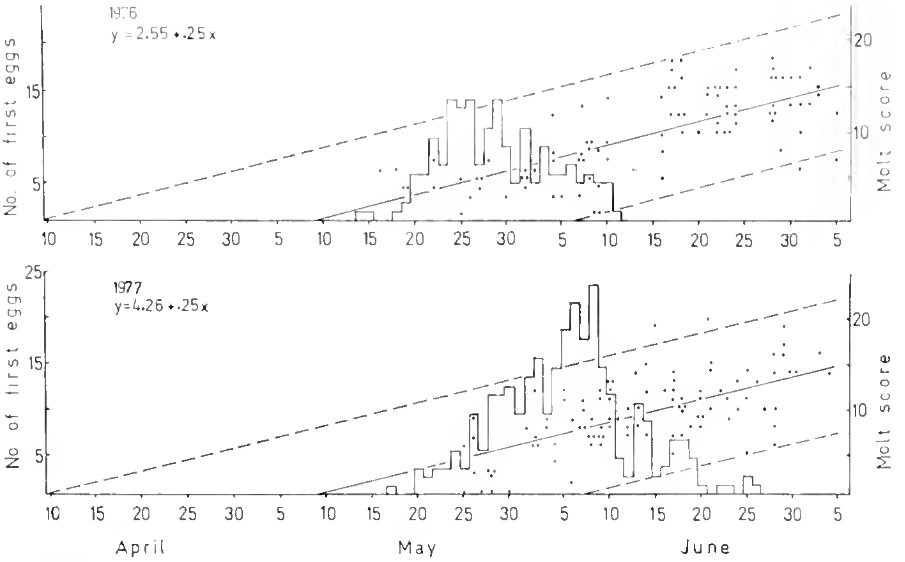

FIG. 1. Molt scores (dots) and the laying date of first eggs (histograms) of *Larus glaucescens* on Mandarte Island. Each dot represents the molt score of 1 bird. The solid, slanted line indicates the progress of molt in time and the regression equations apply to this line. The outer, broken lines represent the approximate temporal limits within which primary molt in the population occurs.

In 1976 only 3 gulls were caught that had not yet begun to molt. The molt scores of 96 birds in 1976 and 98 birds in 1977 indicate that on the average molt in the population began on 9 May in both years (Fig. 1). I estimate that molt in some individuals began as early as 10 April (Fig. 1). On my first arrival on the island on 23 April 1977, shed first (innermost) primaries were found scattered throughout the gullery. Assuming a steady

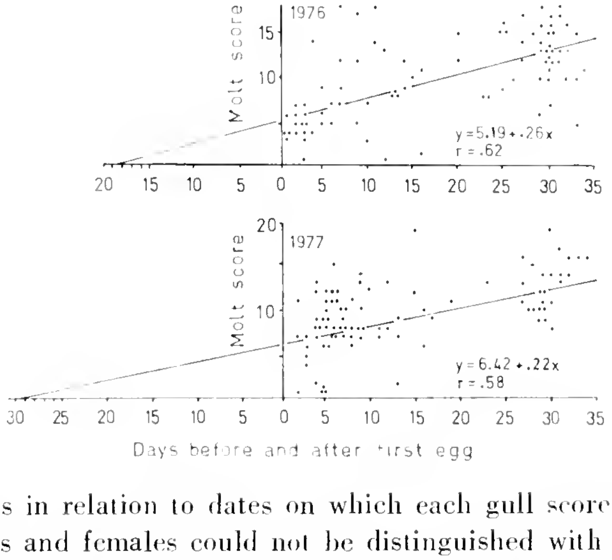

FIG. 2. Molt scores in relation to dates on which each gull scored laid its first egg in 1976 and 1977. Males and females could not be distinguished with certainty. Where the regression lines intercept the x-axis indicates the average day in each year on which molt began prior to egg-laying.

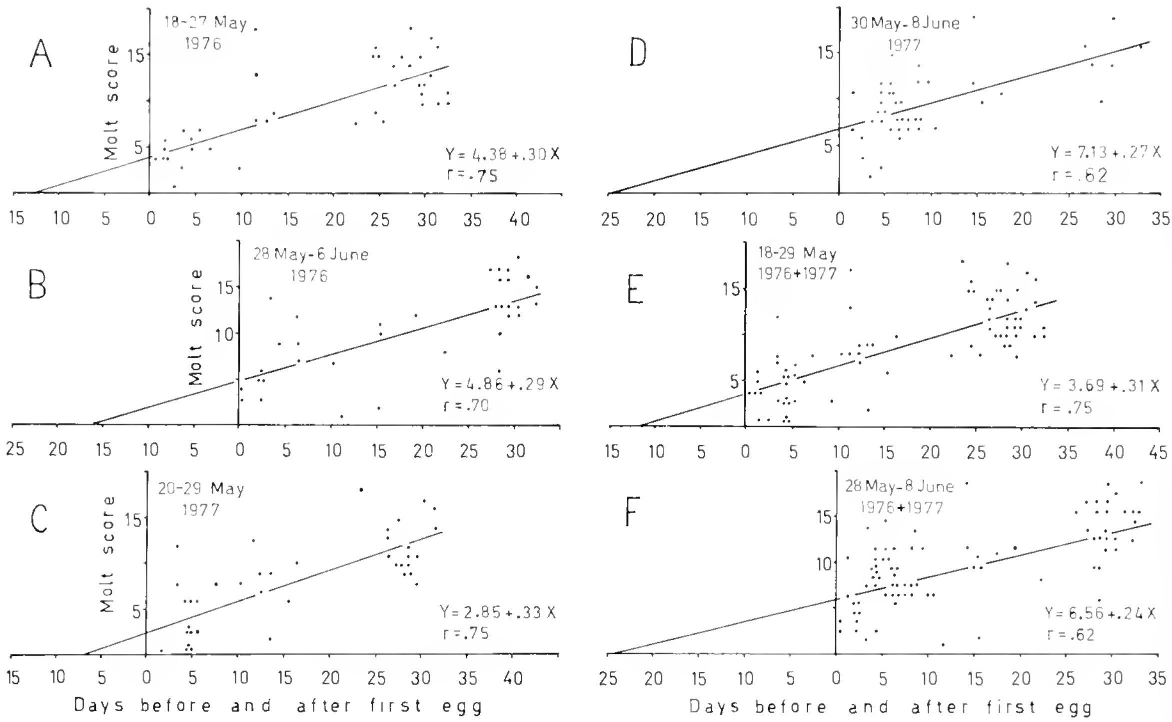

FIG. 3. Molt scores in relation to dates on which each gull scored laid its first egg in 1976 (A and B) and 1977 (C and D). For each year first-egg-dates have been divided into 2 consecutive 10-day-periods. Too few gulls were caught and their molt scored beyond 6 June 1976 and 8 June 1977 to warrant inclusion of a 3rd 10-day-period for each year. Diagram E shows the combined molt scores of A and C, and diagram F shows the combined molt scores of B and D.

rate of feather replacement, primary molt in the population should be completed in 8.5 months, and in the individual in about 6.5 months.

On the average, inception of primary molt in an individual occurred 22 days before the laying of the first egg in 1976, and 34 days in 1977 (Fig. 2). When molt scores of individuals were plotted in relation to when they laid their first egg (presented in 2 consecutive 10-day periods for both years in Fig. 3), it appeared that birds which laid in the first 10-day calendar period did not on the average begin to molt their primaries earlier than birds which began to lay in the following 10-day period (Fig. 3).

DISCUSSION

Glaucous-winged Gulls on Mandarte Island maintain different molt schedules in relation to egg-laying than do Herring Gulls on Walney Island (Verbeek 1977). Both islands have a humid mesothermal climate (Cbf in the Köppen system) and they are located at approximately the same latitude. Mandarte Island is about 400 km farther south than Walney Island, but this cannot explain the differences noted.

Whereas in Herring Gulls on Walney Island egg-laying preceded primary molt, and incubation only barely overlapped with the onset of primary molt (Verbeek 1977), on Mandarte Island the average day of inception of primary molt preceded the mean date of egg-laying by 19 days in 1976 and 27 days in 1977. Although the average day of inception of molt was the same in both years (9 May), the mean date of laying of first eggs was 8 days later in 1977 than in 1976 (Fig. 1). Hence the difference between the 27 days in 1977 and the 19 days in 1976 mentioned above. These same differences in timing between the average day of initiation of molt and egg-laying are shown in Fig. 2 where the molt scores are presented in relation to a common time base. The Glaucous-winged Gull thus resembles the Glaucous Gull in Alaska (Johnston 1961) in which, according to my extrapolation, molt in the population began about 1 May, while egg-laying began on 19 May. Similarly, Glaucous Gulls on Iceland may begin to molt prior to egg-laying (Ingolfsson 1970).

Stresemann (1971) pointed out that in gulls molt and egg-laying are not mutually exclusive. This is confirmed in this study (Figs. 2 and 3). Although the continued cool weather in 1977 produced a significant delay in the mean date of laying of first eggs compared with 1976, the average date of onset of primary molt was the same for both years (Fig. 1). Hence, cool temperatures as such do not appear to affect the onset of primary molt. This suggests that the ultimate factor—day length—exerts control over the beginning of molt in this species.

Herring Gulls (Mayr 1963) and Glaucous-winged Gulls are probably of arctic–subarctic origin. It would be inconsistent to suggest that Glaucous-winged Gulls have maintained their northern molt schedules while Herring Gulls have not. Molt schedules are adapted to local selection pressures and they must fit adaptively in the annual cycle of a species. For instance, with a recent change from migrant to resident status in some Lesser Black-backed Gulls in England, an apparent forward shift has occurred in the timing of primary molt. Resident Lesser Black-backed Gulls appear to molt earlier than migrant individuals (Verbeek 1977). If the Glaucous-winged Gull on Mandarte Island has maintained its arctic molt schedule, the persistence of this schedule must be dictated by local conditions.

The duration of primary molt in the individual Glaucous-winged Gull on Mandarte Island is about 195 days. Similar data for the Glaucous Gull and the Great Black-backed Gull (*L. marinus*) is 205 and 188 days respectively (Ingolfsson 1970). In contrast, Herring Gulls molt their primaries in about 120 days (Harris 1971, Barth 1975, Verbeek 1977). The Glaucous-winged Gull, about equal in size to the Herring Gull, thus requires 75 days longer to molt its primaries than does the Herring Gull.

If the timing of molt and egg-laying, and the duration of molt, is geared to the proximate factor of food availability, and for many birds this seems to be the case (Payne 1972), then it appears that in the population studied here the initiation of molt is geared to a different food supply than the one to which the breeding cycle is geared.

Herring Gulls on Walney Island and Glaucous-winged Gulls on Mandarte Island feed on garbage (Shaffer 1971, Henderson 1972, pers. obs.). This is available all year round and it is not likely to affect the beginning of molt. If it were important, then Herring Gulls on Walney Island should have started to molt earlier than they did. A more likely candidate is fish. To my knowledge little is known about which species of fishes are eaten by Herring Gulls on Walney Island. Early molting on Mandarte Island may be possible because of the early spawning of eulachons (*Thaleichthys pacificus*). Spawning occurs on nearby mainland rivers, such as the Fraser River, from mid-March to mid-May (Andrews 1973). Commercially, most eulachons are caught in March and April (British Columbia Catch Statistics 1969). Glaucous-winged Gulls feed extensively on this species (Hart and McHugh 1944, pers. obs.). The main food fed to the Glaucous-winged Gull chicks on Mandarte Island is Pacific herring (*Clupea pallasii*) (Henderson 1972, Ward 1973, pers. obs.). In the general region of Mandarte Island the mean spawning time of Pacific herring falls in the second half of March (Outram and Haegele 1969). Small fry, 40–50 mm are available in shallow water in June and July. Much of the food fed to the gull chicks consists of these small fishes. Henderson (1972) and Ward (1973) consider the natural food supply available to gulls on Mandarte Island inferior compared to other Glaucous-winged Gull colonies. This may well explain the extended period of molt in this gull on Mandarte Island.

SUMMARY

The timing of the primary molt and egg-laying in the Glaucous-winged Gull was studied on Mandarte Island, British Columbia, in 1976 and 1977. On the average molt in the population began on 9 May in both years, but some individuals began to molt primaries as early as 10 April. On the average primary molt in the individual lasted 6.5 months and began 19 days before the laying of the first egg. Cool weather delayed the mean date of laying in 1977 significantly compared with 1976, but it did not influence the mean date of initiation of primary molt. This suggests the importance of the photoperiod in the timing of molt. Egg-laying began in mid-May and the young were in the nest by mid-June. It is suggested that the early start of molt is timed to the spawning of eulachons. The timing of egg-laying is geared to the availability of Pacific herring fry in June and July.

ACKNOWLEDGMENTS

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PREDATION ON RED-WINGED BLACKBIRD EGGS AND NESTLINGS

FRANK S. SHIPLEY

The contents of Red-winged Blackbird (*Agelaius phoeniceus*) nests are subject to extensive and highly variable losses. Normally, most red-wing eggs fail to produce young that are able to leave the nest. Most researchers have found 60 to 100% of the losses to be due to predation on nest contents, where the entire brood or clutch is lost at once. Fewer than 5% of the losses normally appear to be related to starvation of nestlings or nestling competition. The remainder of the losses (under 40%) result from a variety of causes including egg infertility, nest desertion, and nest tipping due to growth of the supporting vegetation. In this study, I relate predatory losses of red-wing nestlings and eggs to water depth at nest-sites, habitat type, and number of young in the nest. My studies were done in east-central Kansas; several previous authors have presented data from similar studies in other parts of the range of the Red-winged Blackbird (Goddard and Board 1967; Robertson 1972, 1973; Case and Hewitt 1963).

METHODS AND STUDY AREAS

Red-wings were studied at 6 areas within 20 km of Manhattan, Kansas. Two upland sites had similar topography and vegetation and were within the Konza Prairie Research Natural Area, south of Manhattan. Each consisted of a draw containing a small stream and the surrounding lowland. Vegetation was of the tall grass prairie type, largely treeless. Red-wings nested in scattered brushy growth, primarily buckbrush (*Symphoricarpos orbiculata*) and willow (*Salix* spp.). Except for one 4 m diameter pool in area A, there was no standing water and no cattails (*Typha latifolia*). A third study area, north of Manhattan, was also designated "upland." It was similar to the Konza areas but contained many young trees and was bordered by farmland.

The remaining 3 areas were designated "marsh." Two of these were on the edges of an old oxbow of the Kansas River, and contained large unbroken stands of cattails and standing water up to 80 cm in depth. In 1974, water completely disappeared by early July in all but 1 corner of one of these areas. The third marsh area was a cattail marsh below the dam at Tuttle Creek Reservoir north of Manhattan.

Data were taken in all areas during the 1974 nesting season, and in the marsh areas in 1975. Red-winged Blackbird nests were located and marked with small flags placed about 10 m from the nest-site. Water depth at the nest-site at the time of discovery was measured, nest contents were noted, and Brown-headed Cowbird (*Molothrus ater*) eggs were removed when present in the nest. Nests were visited on alternate days until the clutch or brood had either suffered catastrophe, been abandoned, or the young had fledged. I include here only nests that were discovered prior to hatching and for which the subsequent history is known.

Brood sizes in most nests were experimentally manipulated by removing nestlings from

1 nest and adding them to another. Nestlings were moved as soon after hatching as possible (usually the same day) and broods were augmented only by nestlings of the same age in days. Thus "augmented" broods had more young in the brood than there were eggs in the original clutch, and "depleted" broods had fewer young. "Natural" broods had the same number in the brood as were present in the original clutch, and included several nests to which nestlings were added at hatching but in which natural brood reductions occurred early in the nestling period.

When a nest was encountered that had been preyed upon since the last visit, observations were made on contents of the nest, condition of the nest, condition of the supporting vegetation, and on predator tracks when they were present. Measures of predation pressure were calculated after Mayfield (1961) as "Number of nests preyed on"/"Number of nest-days exposure" in order to account for finding nests in which eggs had been present for varying lengths of time. Chi-square analysis by Dow's method (1978) was used to determine the significance of differences between predation rates. This method accounts for the fact that the Chi-square test cannot be used on data which are not independent frequency data. Frequencies of successful and preyed-upon nests were calculated from predation pressure values based on 23 days of exposure for the average nest.

RESULTS

Based on signs left by the predators of red-wing nest contents, I categorized predation into 3 types. Type 1 was eggs or nestlings gone with the nest left intact, and was thought to be the result of avian predation, particularly by the Common Grackle (*Quiscalus quiscula*). or occasional predation by snakes, possibly the water snake (*Natrix sipedon*), which is locally common.

Type 2 predation was the nest and supporting vegetation ripped down, with the eggs or nestlings gone. It was thought to be due primarily to raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and to a lesser extent mink (*Mustela vison*). Type 2 was the most distinctive and recognizable type of predation found.

In type 3 predation, the nest was intact, the eggs destroyed, and the egg-shells left in the nest. Type 3 was observable only before hatching and was thought to result primarily from small mammal predation. Type 3 may also have involved avian predation as well and is thus not entirely distinct from type 1. No predation of any type was observed actually taking place.

Predation and water depth.—Total predation on marsh red-wing nests was inversely related to water depth at the nest-site (Table 1, Fig. 1). Predation in water 0–20 cm deep was significantly greater than predation in water 20–40 cm deep ($\chi^2 = 15.6$, df = 1, $P < 0.001$).

The effect of water depth varied for the 3 observed types of predation. Type 2 predation, thought to be primarily raccoon, was the most intense of the 3 types, and steeply decreased with increasing water depth. Type 2 predation in water 0–20 cm deep was significantly greater ($\chi^2 = 14.1$, df = 1, $P < 0.001$) than type 2 predation in deeper water; in fact there were no

TABLE 1

THE EFFECT OF WATER DEPTH AT RED-WINGED BLACKBIRD NEST-SITES ON PREDATION PRESSURE[1]

Water depth (cm)	No. nests	No. nest-days exposure	No. nests preyed upon				Predation pressure			
			Type 1	Type 2	Type 3	Total	Type 1	Type 2	Type 3	Total
0–10	72	917	4	33	12	49	0.004	0.036	0.013	0.053
10–20	68	720	12	10	9	31	0.017	0.014	0.012	0.043
20–30	16	227	1	0	1	2	0.004	0.000	0.004	0.009
30–40	5	69	1	0	0	1	0.014	0.000	0.000	0.014

[1] Predation pressure = no. nests preyed upon divided by no. nest-days exposure.

recorded instances of predation by large mammals in water deeper than 20 cm. Since type 2 was the most intense component of observed predation, water depth effects on type 2 are largely responsible for the overall negative correlation between predation and water depth.

Type 3 predation, thought to result primarily from small mammals, did not significantly decline with water depth ($\chi^2 = 2.4$, df = 1, $P > 0.05$). Type 3 predation was significantly less intense than type 2 in water 0–10 cm deep ($\chi^2 = 12.9$, df = 1, $P < 0.001$) but closely corresponded to type 2 values in deeper water. Type 1 predation, thought to be avian, was also not significantly influenced by water depth ($\chi^2 = 0.1$, df = 1, $P > 0.05$).

The lack of nests in water deeper than 20 cm probably reflects a paucity of suitable emergent vegetation in which to nest. Because there were only 21 such nests, the differences among the predation rates for these nests were subject to relatively great random variation.

Predation in marsh and upland habitat.—Predation differences cannot be meaningfully related to habitat per se, without recognizing variables inherent in the term habitat. Thus consideration of water depth, nesting density, and other potentially important factors should be made, and only then extended to include habitat differences in predation. My data (Table 2) show no significant difference ($\chi^2 = 0.03$, df = 1, $P > 0.05$) between marsh and upland predation. Even when the effects of water disappearing in one of the marsh areas are accounted for by considering only predation before the area completely dried, there is no significant difference between total marsh and upland predation pressure, or between marsh and upland predation of any of the 3 types.

Predation and brood size.—Variation in water depth, season, and predator species identity, unless they are accounted for, tend to obscure effects of brood size on predation rate. To eliminate those effects, I considered only

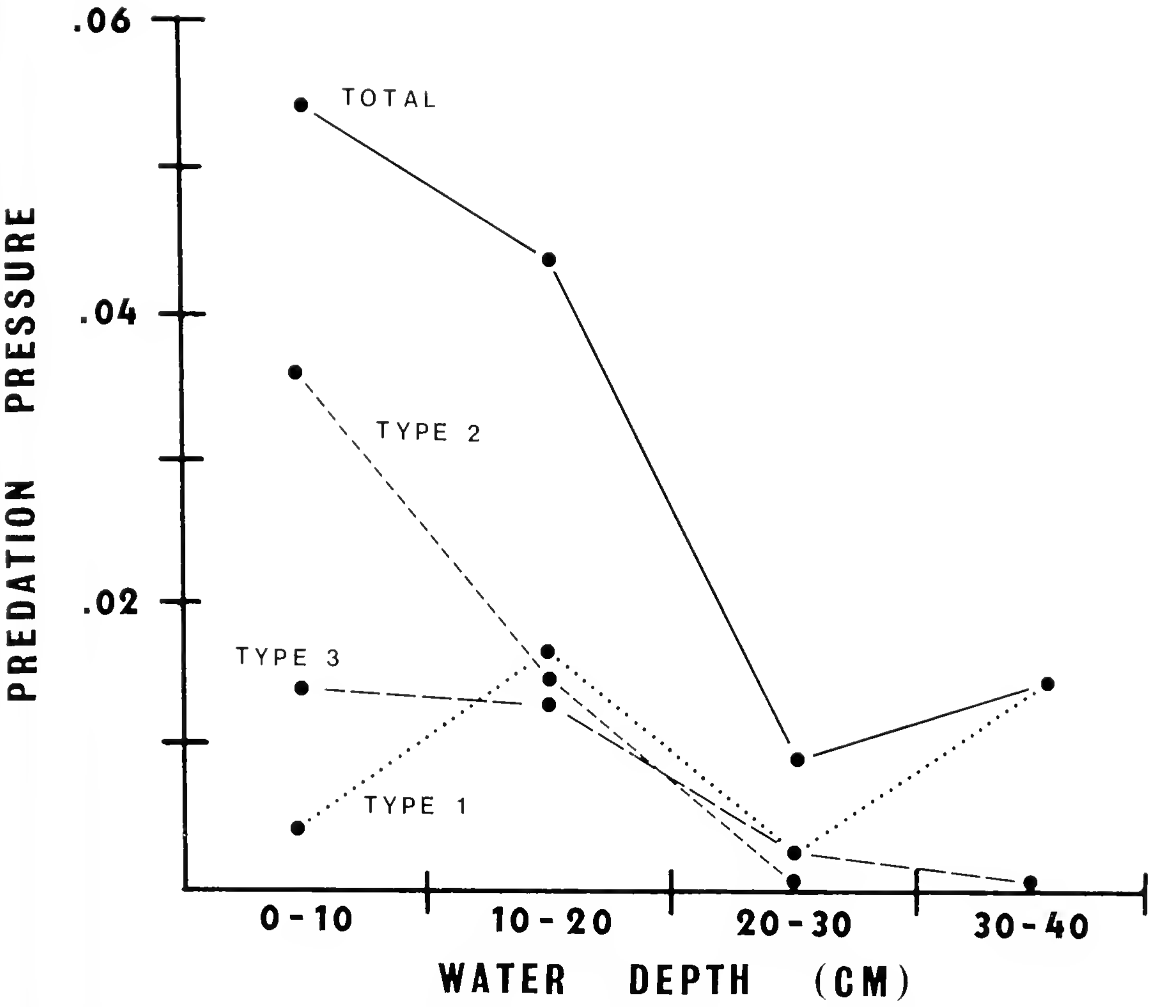

FIG. 1. Predation on the contents of marsh Red-winged Blackbird nests, as a function of water depth at the nest-site.

nests in water less than 20 cm deep, which were relatively available to all predators. Data from the entire season were lumped together to reduce the effect of seasonal changes in the influence of brood size on predation, and predations of the different types were considered separately to account for different predator species types.

TABLE 2

PREDATION ON RED-WINGED BLACKBIRD NEST CONTENTS IN MARSH AND UPLAND HABITAT

Habitat type	No. nests	No. nest-days exposure	No. nests preyed upon				Predation pressure			
			Type 1	Type 2	Type 3	Total	Type 1	Type 2	Type 3	Total
Marsh	161	1933	18	43	22	83	0.009	0.022	0.011	0.043
Upland	33	383	7	6	2	15	0.018	0.016	0.005	0.039

TABLE 3

THE EFFECT OF BROOD SIZE AND BROOD SIZE MANIPULATION ON PREDATION PRESSURE

	No. nests (water depth at site ≤20 cm)	No. nest-days exposure (after hatch)	No. nests preyed upon		Predation pressure	
			Type 1	Type 2	Type 1	Type 2
Brood size: 2	24	180	4	3	0.022	0.017
3	21	142	2	4	0.014	0.028
4	9	64	1	2	0.016	0.031
5	22	165	2	6	0.012	0.036
Brood manipulation category:						
Augmented	25	189	2	7	0.011	0.037
Natural	15	95	2	2	0.021	0.021
Depleted	44	332	8	8	0.024	0.024

Table 3 relates after-hatch predation pressure of types 1 and 2 to the number of nestlings present in the brood and to brood size manipulation. Augmented, depleted, and natural broods are lumped in the "brood size" data. Type 1 predation was negatively, but nonsignificantly correlated with brood size ($r = -0.84$, $P > 0.05$), while type 2 predation was positively and significantly correlated with brood size ($r = 0.96$, $P < 0.05$). The actual number of young present in the nest may not have been as important in influencing predation as artificial manipulation of the number present, but larger sample sizes are needed to determine whether this is so.

DISCUSSION

Water depth at nest-sites was significant in its effect on predation pressure, and the effects were predator-specific. Mammalian predators were deterred increasingly with increasing water depth beneath nests while avian predators were not apparently influenced by the presence of water. Diminishing returns associated with deep-water foraging may correspond to the depth at which mammalian predators must begin to swim, and thus account for the sharp decrease in predation at a depth of approximately 25 cm. My findings agree with those of Robertson (1972), who found a negative correlation between percent red-wing nests preyed on and water depth, and Goddard and Board (1967) who found nesting success to increase with increasing water depth at nest-sites. Francis (1971) in a review of red-wing literature, found no significant difference in nesting success for sites of varying water depth. Because influence of water depth varies with mammalian predator species identity, because avian predation apparently occurs independently from water depth and because non-predatory nest destruction can be significant, overall nesting success will not always be well correlated with water depth. While predation is normally the most important determinant of nesting success, it is not the only one.

Red-wing nesting densities are normally higher in marsh than in upland habitat. Robertson (1973) has found nest densities that differ by as much as an order of magnitude. Thus, in marsh areas with relatively shallow water, predators should be more efficient than upland-searching predators in finding nests. Further, by temporarily specializing on marsh red-wing nest contents as they become seasonally dense, predators could maximize their prey discovery rate. This "switching" in predators (Murdoch 1969) would be enhanced if they are able to form a search image, or key on the activity of the females caring for their hatchlings. My data may reflect such density dependent switching, particularly where, with decreasing water depth, nests became available to mammals. In some cases, signs left at nests preyed upon by raccoons indicated a systematic searching pattern, resulting in nearly complete destruction of the red-wing nesting in the area.

My observations do not support Robertson's (1972, 1973) hypothesis that nesting synchrony and the tendency toward nesting coloniality in marsh sites results in high enough nesting density to satiate predators and thus reduce the probability of predation on each nest in the population. However, I have no density data and may have been dealing with nests in a positive density-dependent predation range, resembling other populations studied by Robertson. More work clearly needs to be undertaken, perhaps in manipulation of nest density.

Water depth and nest density probably constitute important variables in most habitat differences in predation on red-wing nest contents. The frequently observed pattern of higher predation in upland than in marsh sites (Robertson 1972, 1973; Francis 1971; Case and Hewitt 1963) should thus normally be explainable in these terms. The presence of water in marsh habitats may also influence the density of nests by allowing higher nesting densities without corresponding high predation rates. Further, benefits which accrue from the "mobbing" of potential nest predators, a behavioral consequence of the density itself rather than a habitat factor, may make dense nesting even more reproductively advantageous.

My observations indicate that some aspect of brood size or experimental manipulation of brood size affects predation rate. Unfortunately, my sample was not large enough to determine which of these is more important. If clutch-size is adapted to the limits of the female's feeding ability (Lack 1954), adding a nestling could result in a disruptive change in the feeding activity of the female. Brood activity might also be increased due to increased nestling hunger, and in the presence of predators keying on activity at the nest, augmented nests would be subject to increased predation rates. Natural differences in brood size, however, could result in increased feeding activity by the female or increased brood activity, producing the same effect. Since nocturnal predation constituted more than half of the predation I observed, brood activity may have been what attracted predators.

SUMMARY

Predation pressure on the eggs and nestlings of Red-winged Blackbirds was related to water depth at nest-sites, habitat type, and number of young in the nest. On the basis of signs left by predators, predations were classified into 3 types, thought to correspond to avian, large mammal (primarily raccoon), and small mammal predators. Mammalian predation was greater for shallow water nests than for deep water nests, particularly for large mammalian predators, the most important predator type. Avian predation was not significantly influenced by water depth. Total predation on nest contents was not significantly different between marsh and upland situations. Mammalian predation increased with brood size, where some broods were of artificially manipulated size. This pattern may or may not exist apart from experimental brood size manipulation.

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APPENDIX

Predation and season.—Using data from 1974 when both marsh and upland sites were studied, predation pressure was calculated for 5-day intervals over the season (Table 4). Because the maximum number of nests extant during any 5-day period during 1974 was only 20, predation rates varied widely with small differences in the number of nests preyed upon. Because these data show no significant trends, they are included to allow lumping with other small samples in subsequent analysis of predation patterns by other workers.

TABLE 4

THE EFFECT OF DATE ON PREDATION PRESSURE, 1974

	No. nests extant		No. nest-days exposure		No. nests preyed upon		Predation pressure	
Date	Marsh	Upland	Marsh	Upland	Marsh	Upland	Marsh	Upland
June 10–15	12	15	45	65	1	1	0.022	0.015
15–20	17	18	62	80	4	2	0.064	0.025
20–25	20	13	72	49	3	3	0.042	0.061
25–30	18	13	78	54	2	3	0.026	0.055
July 1–5	14	9	65	33	3	1	0.046	0.030
5–10	9	5	30	24	1	0	0.033	0.000

REQUEST FOR ASSISTANCE

Mississippi Kite color-banding.—Mississippi Kites are being marked with colored leg bands and patagial tags in western Kansas and Oklahoma, and north-central Texas. Each kite carries a Fish and Wildlife band and from 1–3 additional color bands in combinations of red, blue, green, yellow and silver. Kites captured as adults also wear a pair of plastic patagial streamers on the dorsal surface of the wings. Streamer colors are red, dark blue, light blue, orange, yellow, and green; about one inch of each streamer extends beyond the ends of the secondary feathers. Persons observing the marked kites are requested to send as much information about the kite and its situation as possible to: Chief, Bird Banding Office, Office of Migratory Bird Management, Laurel, Maryland 20811. Please send a copy, plus any additional information, to the bander, James W. Parker, Biology Department, State University College, Fredonia, New York 14063.

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RESPONSE TO FOSTER NESTLINGS BY RED-WINGED BLACKBIRDS AT DIFFERENT REPRODUCTIVE STAGES

Larry C. Holcomb

Some investigators have performed experiments on acceptance of foster young in the nests of non-passerines. They report differences in acceptance in such stages as early egg-laying, incubation or prolonged incubation (Breitenbach et al. 1965, Beer 1966, Miller 1972). The only passerine data available were those collected by Emlen (1941) on the Tricolored Blackbird (*Agelaius tricolor*) and by Holcomb (1967) on the American Goldfinch (*Carduelis tristis*). The goldfinches, with a normal incubation of 11–12 days, accepted young after 5 and 19 days of incubation, respectively, and raised them to fledging.

Emlen (1941) reported that Tricolored Blackbirds fed young that hatched in the nest as early as the last day of egg-laying. Nestlings 2–3 days of age were placed in 10 nests where laying had just been completed. Two females abandoned their nests, but 8 females cared for the nestlings. Emlen also showed that females brought very little food to the nest until they finished laying. He concluded that development of breeding behavior in the tricolor is closely regulated by physiological factors from the start of nest-building through initiation of incubation, and largely by external situations associated with the nest during the rest of the cycle.

This paper describes experiments conducted to test the effects of foster nestlings of different ages on parental acceptance in periods of egg-laying, normal incubation, or prolonged incubation in the Red-winged Blackbird (*Agelaius phoeniceus*). This paper will deal with the observation of acceptance, non-acceptance or aggressive behavior toward nestlings followed by acceptance. It does not analyze the intricate behavior of development of brooding and feeding.

My hypotheses were (1) that acceptance of nestlings during the empty nest and egg-laying periods would be the same as during the normal incubation period and (2) that acceptance of nestlings during the prolonged incubation period would be the same as during the normal incubation.

METHODS

Red-wings were studied from 1966–1970 in small marshes and alfalfa fields at Fremont, Dodge Co., Nebraska in 1966; Wooster, Ohio in 1967 and near Waterloo, Douglas Co., Nebraska from 1968–70. Each year several hundred nests were observed. The large number of nests observed provided (1) documentation of normal abandonment rate and (2) nests from which nestlings could be transferred to other nests in different stages.

TABLE 1

DISTRIBUTION OF RED-WINGED BLACKBIRD NESTS IN WHICH EXPERIMENTS WERE PERFORMED WITH FOSTER NESTLINGS

Time in cycle		Day 0–1 nestlings	Day 2–5 nestlings	Day 6–9 nestlings
Nest complete		–	1	1
Egg-laying:	day 1	1	7	4
	2nd to last	3	5	3
	next to last	4	6	4
	last	3	1	2
Normal incubation:	day 1–3	14	1	1
	4–9	9	–	1
Prolonged incubation:	day 13–15	1	1	1
	16–18	3	–	2
	19–22	7	3	5

Females were induced to incubate beyond the normal time by placing artificial eggs of the same size, shape and color as their own into the nests early in incubation.

Nestlings introduced to foster nests were separated into 3 age groups: (1) nestlings that hatched from eggs in the nest or were transferred at day 0 (day of hatching) or day 1, (2) days 2–5, and (3) days 6–9. Nests into which these nestlings were introduced were categorized as shown in Table 1. Transfers of nestlings consisted usually of the normal brood size of 3 to 4 nestlings but occasionally of only 1 or 2.

Altogether, 140 transfers of young were made but inconclusive results were obtained in 46 cases, primarily due to predation or severe climatic conditions. Nestlings remained in the foster nest until acceptance or non-acceptance was established in studies from 1966–1969. As there were 3 cases of severe aggressive behavior toward young in those 4 years, I adopted a different procedure in 1970 to protect nestlings from injury. I placed nestlings in a foster nest for a 3–5 h period and either watched the nest from a concealed point or returned to it and removed the young. There were no cases of aggressive behavior in 1970. In all 5 years of the study, nestlings in foster nests were examined carefully each day following their introduction to determine whether or not they had been injured, fed or brooded by foster parents. For statistical evaluation of these data I used a Chi-square test of independence.

RESULTS

There were only 5 nests of a total of 94, or 5.3% of the foster nests, where the nestlings were abandoned or were pecked severely by the adults (Table 2). I do not know whether the nestlings were attacked by the male or female. The female is more suspect as males seldom visited the nests.

Table 2 shows that 4 of the 5 cases of abandonment or severe aggression came just previous to or during the egg-laying period. Table 2 shows the

TABLE 2

RELATIONSHIP BETWEEN REPRODUCTIVE STAGE AND FREQUENCY OF AGGRESSION TOWARD, OR ABANDONMENT OF FOSTER NESTLINGS BY RED-WINGED BLACKBIRD FEMALES

Stage	No. of nests	Severe aggression (%)[a]	Abandonment (%)
Egg-laying (immediately before or during)	45	6.5	2
Normal incubation	26	0	0
Prolonged incubation	23	0	4

[a] These nestlings were gradually accepted even though attacked when first placed in the nest.

1 other abandonment, which occurred on day 18 in prolonged incubation. Three of the 4 cases that occurred previous to normal incubation involved an aggressive pecking of the nestlings by a parent previous to the time when egg-laying ceased and the incubation phase of the cycle began. The nestlings were later accepted and raised to fledging. The other case involved abandonment.

There was 100% acceptance of nestlings transferred to nests during the normal incubation period. We failed to reject the hypothesis that acceptance of nestlings previous to normal incubation was the same as during normal incubation ($P > 0.05$). We failed to reject the hypothesis that acceptance of nestlings during the prolonged period of incubation was the same as during the normal incubation ($P > 0.05$).

From a total of 94 nests, there were only 2 females that abandoned nests with foster young. There was no observed aggressive behavior in either case. From records of several years of field research on Red-winged Blackbirds I have no evidence of females abandoning nests because of my visits. The only nests that were abandoned were those where eggs were removed by a predator, eggs were broken by a predator or the female was captured by a predator. It is not unreasonable to suspect that 1 or 2 females from a total of 94 could have been killed by predators. It would be less reasonable to believe that both females were killed on the day when foster young were placed in the nest.

There was no trend established in acceptance of nestlings on the basis of age differences. However, some brief observations suggested that brooding and feeding of older nestlings were interfered with because of size. The females appeared frightened by the larger nestlings and initial feeding began after a longer elapsed time than with smaller nestlings. Although in most cases older nestlings were accepted (not injured and some feeding and brooding done), often they lost weight because feeding rate was not sufficient. In some cases 1 or 2 of a group of 3 or 4 perished from starvation. When nestlings 5 days or less of age were introduced into 70 different nests, they appeared to receive sufficient food to maintain growth except in the 1 case of abandonment and in 1 case where day 5 nestlings were introduced on the first day of egg-laying.

In all 43 cases where nestlings were transferred to foster nests during egg-laying, even though the nestlings were brooded or fed, the female continued to lay until her full clutch was completed.

DISCUSSION

Holcomb (1968, 1970) reported that Red-winged Blackbird females incubate a mean of about 19 days on artificial eggs of normal or 1½× normal size, even though the normal incubation period is only 11 days. However, they incubate eggs ½× normal size an average of about 15 days, suggesting that red-wings do react to either a visual stimulus, a tactile stimulus or a combination of stimuli from the eggs.

The greater amount of data on abandonment collected for the red-wing during egg-laying and normal incubation appears similar to the limited data provided for Tricolored Blackbirds by Emlen (1941). There is no evidence of a difference in abandonment when comparing (1) egg-laying and normal incubation or (2) normal incubation with prolonged incubation.

When younger nestlings were introduced to foster nests they appeared to receive sufficient food. Older nestlings sometimes were accepted and fed but grew more slowly than they would have in their original nests. Some perished, indicating inability of the female to adjust quickly to the demands of large nestlings. My data suggest that feeding behavior must develop quantitatively with the development of nestlings, beginning slowly and increasing as nestlings grow older and demand more food.

In more than 1 case, when I placed older nestlings in nests, they were accepted and fed for 1–2 days before fledging, whereupon the female spent at least part of her time incubating the eggs again. I do not know whether these females fed the fledglings enough to maintain them, whether the male fed them, or if they perished.

There are some differences between passerines and some non-passerines in acceptance of foster young early in the incubation period. Evidence presented herein for all passerines tested to date shows acceptance of foster young early in the incubation period in the Tricolored Blackbird, American Goldfinch and Red-winged Blackbird. This is in contrast to a report by Breitenbach et al. (1965) on the response of hen Ring-necked Pheasants (*Phasianus colchicus*) to chicks introduced during normal or prolonged incubation. None of 3 hens accepted chicks 12 days early, 3 of 8 accepted them 8 days early and 7 of 7 accepted them 4 days early. Four of 4, 6 of 6 and 2 of 2 accepted chicks 4, 8 and 12 days late, respectively. Miller (1972) reported that in Ring-billed Gulls (*Larus delawarensis*) when chicks were introduced in the first week of incubation, acceptance was irregular and temporary but that parents accepted chicks introduced after 8 days. When Emlen and Miller (1969) delayed hatching of Ring-billed Gulls only 3 to 8 days, 3 of 12 sets of parents abandoned the nests or tossed the chicks out of the nest. Of 14 cases of acceptance reported by Miller (1972) from a total of 24 experiments, 16 chicks were initially pecked by adults.

I do not intend this paper to be a complete review of endocrinological factors controlling the onset of parental behavior. However, since there was some aggression toward foster nestlings in the egg-laying period, some comment on endocrinological factors is appropriate.

Brant and Nalbandov (1956) documented the effect of estrogen and progesterone on oviduct growth in chickens. Lott and Comerford (1968) demonstrated in Ringed Turtle Doves (*Streptopelia risoria*) that initiation of parental behavior may be due to a combined effect of progesterone and prolactin; progesterone alone established brooding, while progesterone plus prolactin caused both brooding and feeding. Hansen (1966) reported the effect an external stimulus (the squab) has on prolactin production and/or release in Ringed Turtle Doves. In pigeons (*Columba* spp.) (Schooley 1937), hens (*Gallus* spp.) (Collias 1950), House Sparrows (*Passer domesticus*) (Vaugien 1955), Bank Swallows (*Riparia riparia*) (Petersen 1955), Tricolored Blackbirds (Payne 1969) and White-crowned Sparrows (*Zonotrichia leucophrys*) (Lewis 1975), the ovary has been reported to be regressed during the incubation period. Meier (1969) has shown the antigonadal effects of prolactin in White-throated Sparrows (*Zonotrichia albicollis*).

I found (Holcomb 1975) that red-wing females exhibit great changes in incubation patch tissues as nest building, egg-laying, normal incubation and prolonged incubation proceed. I showed (Holcomb 1968) that in the egg-laying period of red-wings, estrogen and perhaps progesterone are abundant as evidenced by large ovary size and large size of the oviduct. As soon as laying ceases, ovary and oviduct regress rapidly and remain small until 2–4 days past the length of the normal incubation period. Small increases in ovarian weight begin, and there is a significant increase in size of the oviduct and of ovarian follicles, previous to abandonment of the eggs in the prolonged incubation period.

I believe that prolactin suppresses ovarian size in and maintains incubation in red-wings following ovulation. I believe that the large size of the ovary when a nest has been constructed or when eggs are being laid indicates that prolactin is not present in quantities sufficient to have an antigonadal effect on the ovary. I have shown (Holcomb 1974) that incubation develops gradually in the red-wing female throughout the egg-laying period. This may indicate initially small amounts of prolactin that gradually increase, finally causing rapid antigonadal effects after all large ovarian follicles have ovulated. During this dramatic change in internal stimuli and in environmental stimuli such as new nest and new eggs, there is a transition period when the female may be aggressive toward nestlings, abandon them or fail to feed them sufficiently to maintain growth.

Throughout the normal incubation period the antigonadal effect of prolactin continues, and incubation constancy is highest. As the female progresses into a prolonged incubation, prolactin remains an antigonadal agent; but as it slowly diminishes, the ovary begins growing again and is active in releasing a hormone or hormones as evidenced by the increase in size of the oviduct. At this time females are still capable of accepting nestlings, as prolactin still has some influence. Furthermore, a transition from the now-familiar nest and eggs to new stimuli (the nestlings) may be an easier behavioral adjustment than during the early portion of the nesting cycle.

Evidently, as long as incubation continues, prolactin is sufficient for the acceptance of red-wing nestlings, even though their initial food demands cannot always be met. Emlen and Miller (1969) suggest that once normal incubation has been established, internal stimuli may play a role but may not be as important as external stimuli. These hypotheses await testing through continued studies.

SUMMARY

Experiments were performed with Red-winged Blackbirds (*Agelaius phoeniceus*) at different reproductive stages to determine the frequency of parental acceptance of nestlings. Nestlings aged 0–1, 2–5, and 6–9 days were placed in nests where the nest was complete without eggs and when the last, next to last, and second to last eggs had been laid. Nestlings of these different groups were also placed in nests during normal and prolonged incubation.

There appeared to be no great differences in ability of females to accept any age group of nestlings. However, during the egg-laying period most females fed nestlings sparingly and sometimes were aggressive toward nestlings. The frequency of acceptance of nestlings did not differ significantly between (1) normal incubation and egg-laying periods and (2) normal incubation and prolonged incubation periods ($P > 0.05$). The internal physiological mechanisms and the external stimuli that may account for the observed differences in behavior are discussed.

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NESTING ECOLOGY OF THE EASTERN PHOEBE IN SOUTHERN INDIANA

Harmon P. Weeks, Jr.

The Eastern Phoebe (*Sayornis phoebe*), a common summer resident in southern Indiana, makes extensive use of bridges and culverts for nesting throughout most of the eastern United States. This adoption of man-made structures has allowed expansion of breeding populations far from their primeval nesting habitats and may offer increased security from terrestrial predators. Nest success, however, may be adversely influenced by human and livestock disturbance. Nests on artificial structures frequently must adhere to vertical elements, with the resulting increased likelihood of falling.

Although Eastern Phoebe nests are easily detected and readily accessible, many aspects of phoebe nesting biology are poorly described. Kendeigh (1952) commented on this paradox, yet little has been accomplished since then. In an attempt to fill some information voids on the breeding biology of this species in the Midwest, I studied a nesting population of Eastern Phoebes in an unglaciated portion of southern Indiana in 1970 and 1971. Special emphasis was placed on evaluating use of and quantifying various success parameters in nests on bridges and culverts in a region of abundant natural nest-sites. An additional objective was to identify the importance of old nests remaining from previous seasons and nest placement on nesting success. Only a few nests in natural locations were examined. No birds were marked.

METHODS

This study was conducted on Crane Naval Weapons Support Center (Crane NWSC), a 251 km^2 area occupying the northern third of Martin County in south-central Indiana. About 25% of the area is composed of old fields, maintained roadsides and other openings, and industrial complexes; the remaining area is wooded. The combination of 3 dendritic stream systems and 650 km of roads provides many bridges and culverts for potential nest-sites.

In February 1970, I inspected all bridges and culverts on the study area for old Eastern Phoebe nests, numbered each nest found, and recorded its condition and location. Other potential nest-sites such as buildings and rock outcrops near roads also were examined. I visited sites at 5–7 day intervals after the first phoebes arrived and recorded nest contents, evidences of new building, and behavioral data. Sites of examined nests included: concrete bridges, creosoted wood bridges, wood and I-beam bridges, concrete culverts, pipe culverts, rock culverts, buildings, natural (rock outcrop), and miscellaneous. I considered any span longer (i.e., linear road distance) than 4 m a bridge and less than that a culvert. After the 1970 nesting season, I removed all old nests to assess the effect of a lack of existing nests on productivity and nest placement parameters in 1971. This removal eliminated the possibility of separating the effect of presence of old nests from the effect of time in the 1971 nesting season. Data collection in 1971 was similar to 1970.

Because phoebes occasionally began several nests at different locations under a bridge or completed a nest without depositing eggs, all nest success calculations were based on nests known to have received at least 1 egg. A successful nest is defined as one that produced at least 1 fledgling. Nest data were sorted by parameters to be compared, and because of nests with missing data, totals in some comparisons are not the same as in others. All nests with clutches initiated on or before 15 May were classified as early season nests; the remainder were late season nests.

Significance in nest reuse and clutch-size was tested with the Student's *t*-test; all other comparisons were with the χ^2.

RESULTS AND DISCUSSION

Arrival and nest building.—I first observed Eastern Phoebes on the study area on 17 March 1970 and 12 March 1971, when males were singing on territory at bridges that were occupied continuously thereafter. I found the earliest dates for the beginning of nests in 1970 and 1971 to be 2 April and 27 March, respectively. Early season construction of a new nest or renovation of an old one usually took at least 7–8 days and at times as long as 10–12 days. Temperature seemed to be a strong controlling factor during this period; regardless of construction stage, building would often cease completely during days when temperatures were below ca. 10°C. Since nest building seems to be under partial control of temperature, seasonal variation in nest initiation could be considerable. Nests that were evidently complete regularly stood empty for 1–9 days prior to egg-laying (Weeks 1978). Nest construction after mid-May took as little as 5 days for complete construction and 3 days for renovation of existing nests ($\bar{x}$ = 10.5 days between fledging and new clutch initiation).

Nest placement and type.—Phoebes built both statant and adherent nests. They often depended on some surface irregularity (e.g. nails, wire, rough concrete, wood splinters, mud dauber [*Trypoxylon politum* or *Sceliphron caementarium*] nests) for initial attachment of nest material for adherent nests, yet the early stages of building in these nests were more difficult than for statant nests. The female, for only females build (Smith 1942), had to hover at the nest-site and "throw" mud against the surface with a flick of her head. This continued until enough of a base was built up to allow perching. Adherent nests were thus characterized by a circle of small mud splashes radiating from the nest.

Adherent nests were more common than statant nests under both bridges (56.1% vs 43.9%) and culverts (66.7% vs 33.3%). Nevertheless, it cannot be concluded that Eastern Phoebes preferred adherent to statant nests, since availability of suitable sites had an overriding effect. A high percentage of culvert nests were adherent, but there were very few sites for statant nests. Almost all bridges had many potential statant sites, but frequently not in preferred locations. In many concrete and creosoted wood bridges structural elements at bridge supports provided most of the "shelf" situations but these were rarely used. Nests placed in these locations faced across stream flow and parallel with the roadway. Where possible, phoebes strongly preferred to face nests toward the bridge edges. Drainpipes from the road surface, protruding at 90° to 135° from vertical, were the most common support (14 of 17) for statant nests under concrete bridges. In 1971, only 51.7% of nests built under bridges were adherent. The approximately equal distribution of the 2 types of nests may have resulted from the need to construct entirely new nests and the vacancy of a number of preferred statant sites (because of old nest removal), as well as the apparent relative ease of statant construction.

Nests were built on a variety of structures, although the majority were on bridges and culverts (Table 1). All bridges and culverts were associated with maintained roadside vegetation; however, no bridge containing a nest was more than 25 m from a sizable area of woodland. Such an obligatory nest–woodland relationship was suggested by Graber et al. (1974) in Illinois, and Klaas (1970) found in Kansas that some woody vegetation was necessary near nest-bridges.

Culverts vary less in design than bridges, but the smooth vertical sides of concrete culverts required adherent nests. Culverts of corrugated metal pipe of 1–2 m diameter were generally unusable by phoebes unless a construction flaw (e.g., metal strip hanging from top) allowed nest attachment.

For most bridges and culverts, with the exception of pipe culverts, the number of nests and nesting attempts was largely a function of the number of available structures. Only 5 of 21 examined corrugated metal pipe culverts ever had a nest. There was never simultaneously more than 1 active nest on any structure; Ohlendorf (1976) found the same situation in both Say's (*Sayornis saya*) and Black phoebes (*S. nigricans*) in Texas.

In most situations there was somewhat more than 1 nesting attempt per nest (Table 1), which indicates the reuse of old nests for a second clutch; but since a few nests, especially in 1970, received 3 clutches, these data do not accurately reflect the percentage of nests that were reused. Several trends were evident, however. There was significantly more reuse of nests in culverts than on bridges in both 1970 ($t = 6.27$, df $= 60$, $P < 0.001$) and 1971 ($t = 2.49$, df $= 49$, $P < 0.01$). This perhaps reflects differences in availability of old nests from which to choose for a second nesting (higher under bridges than under culverts in 1970) and the number of available sites for the construction of a second nest (judged considerably higher under bridges).

TABLE 1

EASTERN PHOEBE NESTS AND NESTING ATTEMPTS ACCORDING TO LOCATION[1]

	Active 1970			Active 1971		
Nest location	Nests	Nesting attempts	Attempts/nest	Nests	Nesting attempts	Attempts/nest
Bridges	38 (50.7)	47 (47.5)	1.23[3]	30 (50.0)	44 (48.4)	1.46[2,4]
Culverts	24 (32.0)	36 (36.4)	1.50[3]	21 (35.0)	33 (36.3)	1.57[4]
Buildings	6 (8.0)	7 (7.1)	1.16	5 (8.3)	8 (8.8)	1.60
Misc. structures	7 (9.3)	9 (9.1)	1.28	4 (6.7)	6 (6.6)	1.50
TOTAL ARTIFICIAL	75	99	1.32	60	91	1.51[2]
Natural	8	10	1.25	5	7	1.40
TOTAL	83	109	1.31	65	98	1.50

[1] Data for all nests, including those found at stages after initiation; numbers in parentheses are percent.
[2] Significantly ($t = 6.72$, df = 133, $P < 0.001$ for all structures; $t = 9.68$, df = 66, $P < 0.001$ for bridges) larger than 1970 value.
[3] Means significantly different ($t = 6.27$, df = 60, $P < 0.001$).
[4] Means significantly different ($t = 2.49$, df = 49, $P < 0.01$).

Further indication of the possible effect available old nests may have on nest reuse is revealed by comparison of data from 1970, when old nests were available, and 1971, when all old nests had been removed prior to the nesting season (Table 1). Significantly more attempts per nest were made in 1971 than in 1970, both in total nests on man-made sites ($t = 6.72$, df = 133, $P < 0.001$) and in bridge nests ($t = 9.68$, df = 66, $P < 0.001$). This difference is not reflected in culverts, as would be expected from the aforementioned high reuse in 1970.

Eastern Phoebes on Crane NWSC used old nests not only for second broods but also for earlier attempts. Of 55 old nests in varying conditions marked before the 1970 season, 43 (78.2%) were subsequently renovated and used at some time during the season. Reuse of the same nest after an unsuccessful first clutch was not uncommon. Most researchers agree that Eastern Phoebes occasionally or even frequently reuse a nest for second broods (Klaas 1970, Mengel 1965), but no exact frequencies have been provided. I found 34 sites in 1970 and 33 in 1971 on which 2 or more nesting attempts were made; 16 (47.1%) in 1970 and 17 (51.5%) in 1971 were in the same nest. If only instances in which the first nest was successful are considered, 59.3% (16 of 27) and 81.0% (17 of 21) of the second nesting attempts were in the same nest in 1970 and 1971, respectively. The higher reuse in 1971 was at least partially attributable to the pre-season removal of 1970 nests, which eliminated most old alternate sites, although the removal of all nests in 1971 precludes statistical comparison.

I found little evidence to support the postulate that phoebes often build new nests in succeeding attempts to avoid mite infestations (Bent 1942). There was some mortality of nestlings from the northern fowl mite (*Ornithonyssus sylviarum*), but birds at times reused nests in which the earlier fledged young were heavily infested. In 1970 I found that in instances where birds used a different nest for a subsequent clutch, 62% renovated an old nest rather than build a new one. Since mites survive well from season to season in old nests (Klaas 1975), little reduction in risk of mite infestation would be gained from this nest shift.

A tacit assumption here is that a pair of birds that occupied a structure continuously throughout the nesting season was the same pair. Behavior and event sequences indicated this was usually the case; although there was likely some replacement, the frequency of such replacement could not be determined because the birds were unmarked. Klaas (1970) found that 88% of banded Eastern Phoebes remained at the same site (bridge) throughout the breeding season. Ohlendorf (1976) found similar behavior with Say's and Black phoebes but also found some rapid sequential replacement of breeders. However, in my succeeding considerations the assumption of non-replacement of breeders is not critical to the validity of the presentation.

Egg-laying and clutch-size.—Egg-laying and clutch-size variation have been detailed elsewhere (Weeks 1978). The earliest egg was 10 April in 1970 and 9 April in 1971. In both years 2 definite peaks in egg-laying illustrated the characteristic double-broodedness of the species; the early peak for both years was in mid-April, and the late-season peak in 1970 in late May. The second peak in 1971 was inexplicably delayed by about 10 days. The latest that a clutch was begun was 28 June in 1970 and 21 June in 1971.

The average size for 171 complete clutches was 4.73 ± 0.042 (SE) (range = 3–6 eggs; 67.3% = 5 eggs, 94.7% = 4–5 eggs) with no significant differences in clutch-size between years. I found, however, a significant decline ($t = 3.62$, df $= 165$, $P < 0.001$) in clutch-size in late nests (clutches begun after 15 May). Clutch-sizes were substantially lower in some instances where birds built new rather than using old nests and where birds built adherent rather than statant nests (Weeks 1978).

Hatching, fledging and nesting success.—Since I examined most potential sites prior to nest initiation, nearly all nests were known from inception. I therefore include all nests in my measure of nesting success and base the fledging success calculations on total eggs.

Slightly more nesting attempts were made and eggs laid in 1970 than in 1971 (Table 2). Nesting success was higher in 1970, and it is evident that no 1 factor alone caused the decreased 1971 success. Every facet of the reproductive cycle appeared depressed in 1971 compared to 1970. Perhaps

TABLE 2

SUMMARY OF NESTING DATA FOR THE EASTERN PHOEBE ON CRANE NWSC, INDIANA

	1970		1971		Total	
	Number	Percent	Number	Percent	Number	Percent
No. of active nests[1]	99		95		194	
No. of complete clutches	89		82		171	
Total eggs laid	450		417		867	
Eggs per active nest	4.55		4.39		4.47	
Eggs per complete clutch	4.75		4.70		4.73	
Eggs hatched	340	75.6	281	67.4	621	71.6
Eggs hatched per active nest	3.43		2.96		3.20	
Eggs infertile or addled	12	2.7	20	4.8	32	3.7
Eggs lost or abandoned	98	21.8	116	27.8	214	24.7
Young fledged	307		224		531	
Young fledged per active nest	3.10		2.36		2.63	
Young fledged of eggs laid		68.2		53.7		61.2
Young fledged of eggs hatched		90.3		79.7		85.5
Young lost before fledging	33		57		90	
Successful nests	71	70.3	55	57.3	126	64.0

[1] Excludes nests found after hatching.

the high productivity in 1970 resulted in a 1971 population abnormally high in first year birds, which are generally conceded to be less successful breeders than experienced adults (von Haartman 1971, Lack 1966). In addition, the lack of old nests in 1971 could have had an influence.

My limited number ($N = 10$) of exact determinations of incubation period (i.e., last egg laid to last egg hatched) and nestling period ($N = 18$) agreed with most published reports (Graber et al. 1974, Stoner 1939) that 16 days was the modal length for each; Klaas (1975) found an average in-nest period of 18 days for phoebes. In most instances all eggs hatched within a 24-h period. Hatchability of eggs that survived the incubation period was 95.1% for combined years; as with other factors, it was higher in 1970 (96.6%) than 1971 (93.4%).

I found a significantly higher ($\chi^2 = 134.6$, $df = 1$, $P < 0.001$) survival rate for nestlings than for eggs, with 71.6% of all eggs laid hatching and 85.5% of all young that hatched fledging. Using 21 days (including laying) as the average time that eggs remained in nests and 16 days as the average nestling period, I found a loss rate of 1.35%/day for eggs and 0.91%/day for nestlings. Both rates are substantially lower than most reports for open-nesting altricial birds (Knupp et al. 1977, Roseberry and Klimstra 1970). The higher rate of egg than nestling loss is evidently normal in altricial species (Nice 1957) and would be expected, since almost all nestling losses are to predators, but many agents cause egg losses.

Similarly, slightly more nests failed in the egg (52.4%) than the nestling (47.6%) stage. The pattern of nest failure suggested that once the egg-laying and early incubation period was completed, the nest was relatively secure until hatching. Nearly 35% of unsuccessful nests failed during egg-laying or very early incubation, while only 14% of the failures occurred from that point through hatching. This loss pattern might be predicted since abandonment was most common in this early stage, and the most readily seen and accessible nests would be taken quickly by opportunistic predators. After hatching, the feeding activity of the adults could attract predators to the more concealed nests. The daily nest mortality rate was 0.97% based on a 37-day period (including 5-day laying period), considerably less than the 2.4% average calculated by Ricklefs (1969) for open-nesting passerines.

Nice (1957) found that nesting success in open-nesting altricial birds in the North Temperate Zone averages 49% (46% fledging success). Though she gave no mean, she stated that nesting success in hole-nesting birds was substantially higher with a fledging success of 66%. Nesting success for the Eastern Phoebe might be intermediate between these extremes, since it builds an open nest under protective cover. Nesting success for both years combined was 64.0%, slightly lower than the 66.7% figure for dated nests. This success is similar to the mean success for hole-nesters given by Nice (1957), which is itself probably an inflated value (Mayfield 1961). Success based on dated nestings was significantly ($\chi^2 = 13.1$, df = 1, $P < 0.001$) higher in 1970 than 1971 (Table 3). Graber et al. (1974) found substantially lower nest success for central and southern Illinois phoebes (36–57%), as did Klaas (1970) in Kansas (52%) for nests not parasitized by Brown-headed Cowbirds (*Molothrus ater*). Possible reasons for the difference in success on Crane NWSC and other areas include variations in nest-sites and predator populations. The lack of human and livestock interference on Crane NWSC undoubtedly also played a role. As observed by Nice (1957), fledging success, based on total eggs laid, was lower than nesting success, based on total nests (Table 2). However, differences were small because infertility was low, overall success was high, and predators tended to take complete clutches or broods.

Success parameters (hatching, nestling and fledging) were all significantly higher ($\chi^2 = 13.6$, $\chi^2 = 23.6$, $\chi^2 = 38.1$; df = 1, $P < 0.001$, respectively) in 1970 than 1971 (Table 2). Additionally, nestling success was higher ($\chi^2 = 112.0$, $\chi^2 = 39.0$; df = 1, $P < 0.001$; 1970, 1971, respectively) than hatching success in both years. When only successful nests are considered, the infrequency of partial nesting failure is evident; for combined years, hatching success was 92.8% and nestling success 98.0%. Even in the relatively lower

TABLE 3

NESTING SUCCESS FOR EASTERN PHOEBES ON CRANE NWSC, INDIANA, CATEGORIZED BY SEASON AND NEST SITE[1]

	1970			1971		
	Early (%)	Late (%)	Total (%)	Early (%)	Late (%)	Total (%)
Bridges	16/21(76.2)	15/21(71.4)	31/42(73.8)	14/22(63.6)	13/21(61.9)	27/43(62.8)[2]
Culverts	13/18(72.2)	12/16(75.0)	25/34(73.5)	10/17(58.8)	4/13(30.8)	14/30(46.7)
Misc. structures	5/5(100.0)	5/7 (71.4)	10/12(83.3)	5/6 (83.3)	2/4 (50.0)	7/10(70.0)
Natural	1/3 (33.3)	4/5 (80.0)	5/8 (62.5)	2/3 (66.7)	3/4 (75.0)	5/7 (71.4)
TOTALS	35/47(74.5)	36/49(73.5)	71/96(74.0)	31/48(64.6)	22/42(52.4)	53/90(58.9)

[1] Sample population includes all nests found before hatching in which date of first egg was known, early season = 1 April–15 May, late season = 16 May–30 June.

[2] Success significantly higher ($\chi^2 = 6.7$, df = 1, $P < 0.01$) than for 1971 culvert nests.

hatching success figures, most of the failure to hatch was attributable to egg infertility rather than egg disappearance.

Nesting success for both years combined differed very little between early (69.5%) and late (63.7%) seasons. The difference is almost totally attributable to a moderate late season decline in success in 1971; success was almost identical in both seasons of 1970 (Table 3). Graber et al. (1974) also found a decline in nesting success in the late season in southern Illinois (their division of seasons was identical to mine). This apparent decline of nesting success with time is contrary to the situation found in most altricial species (Nolan 1963, Longcore and Jones 1969, Roseberry and Klimstra 1970). In addition, fledging success also tended to be higher in the early than late season; no general monthly decrease in fledging success was evident, with May having the highest success for any month in 1970 and lowest in 1971 (Table 4). Fledging success was, however, always highest in the months and seasons when the greatest number of eggs were laid.

Longcore and Jones (1969), citing entomological data (Holling 1961), suggested that a partial explanation for low success in Wood Thrushes (*Hylocichla mustelina*) in the early season when many nests were active might be a functional response by predators, i.e., to take a higher proportion of prey when more are available. This concept cannot be accepted as an axiom in vertebrate communities (Smith 1974). Phoebes do not depend on vegetative concealment for nests, and it appears that predator responses to prey (egg and young) density differ between nesters in this niche and species nesting in vegetation. Most passerines use vegetation for nesting cover, which should afford greater concealment as the season advances (Lanyon 1957, Longcore and Jones 1969); cover for phoebe nests does not change appreciably. Gulls

TABLE 4

ANALYSIS OF NESTING SUCCESS COMPONENTS BY TIME PERIOD FOR EASTERN PHOEBES ON CRANE NWSC, INDIANA

		Hatching success		Nestling success		Fledging success	
Year	Division	ratio[1]	%	ratio[1]	%	ratio[1]	%
1970	April	121/177	68.4	116/121	95.9	116/177	65.5
	May	151/189	79.9	133/151	88.1	133/189	70.4
	June	68/84	81.0	58/68	85.3	58/84	69.0
	Early (1 April–15 May)	170/226	75.2	160/170	94.1	160/226	70.8
	Late (16 May–30 June)	170/224	75.9	147/170	86.5	147/224	65.6
1971	April	156/210	74.3	134/156	85.9	134/210	63.8
	May	33/66	50.0	23/33	69.7	23/66	34.8
	June	92/141	65.2	67/92	72.8	67/141	47.5
	Early (1 April–15 May)	165/231	71.4	139/165	84.2	139/231	60.2
	Late (16 May–30 June)	116/186	62.4	85/116	73.3	85/186	45.7

[1] For hatching = no. of eggs hatched/no. of eggs laid, for nestling = no. of young fledged/no. of eggs hatched, for fledging = no. of young fledged/no. of eggs laid.

(*Larus* spp.) laying at the peak of the nesting season are more successful than those laying earlier or later (Patterson 1965, Brown 1967). Though it is difficult to segregate colony effects, the similarity of these gull and phoebe data may be more than coincidental. Given species that depend on structural or geomorphological concealment and/or relative inaccessibility of nests as predator defenses, and given a relatively stable predator population with limited mobility, a constant number of nests would be taken regardless of the number available, i.e., a smaller proportion as numbers increase. This evidently occurs in this Eastern Phoebe population.

For both years combined, nesting success appeared higher in statant (69.0%) than adherent (61.3%) nests though the difference was not statistically significant; this apparent elevated success was general in seasonal and yearly breakdowns. In 1971, success for statant nests (65.2%) was significantly ($\chi^2 = 4.1$, df = 1, $P < 0.05$) higher than for adherent (51.1%). Statant nests had slightly higher overall fledging success than adherent nests, 64.0% and 60.4%, respectively. This difference was not consistent between years, with adherent success higher in 1970 (70.6% vs 66.7%) and statant in 1971 (61.6% vs 47.3%). For all successful nests, however, fledging success was highest ($\chi^2 = 8.0$, df = 1, $P < 0.01$) in adherent nests (93.4% vs 88.1%). This elevated success was consistent between years and was contributed to by both hatching and nestling success. This may indicate that nest predators that usually take single eggs (e.g., *Peromyscus* spp.) can more easily reach statant nests, as would be expected. Other losses in adherent nests must be proportionately higher.

Although adherent outnumbered statant nestings (106 vs 87), my overall impression was that if a suitable statant site was available it was preferred. These success figures, as well as clutch-size data (Weeks 1978), indicate that a preference for statant sites has definite adaptive advantages, although these remain unknown.

Because of numerous factors, most related to susceptibility to nest predation, certain nest-sites seem to be more secure than others (Nice 1957, Cody 1971, Knupp et al. 1977). With phoebes, one might expect nest success to be higher on bridges than in culverts, because culvert nests average much lower and closer to the stream, thus increasing their availability to opportunistic ground predators. This does not seem to have been the case in 1970, for success appears almost equal (Table 3). In 1971, however, success was significantly lower ($\chi^2 = 6.7$, df = 1, $P < 0.01$) in culverts; the difference was especially evident late in the season.

Fledging success was slightly higher on bridges (60.9%) than in culverts (57.5%). However, the success was not consistent between years, with culvert success higher in 1970 (71.6% vs 63.3%) and bridge success higher in 1971 (58.2% vs 41.0%). For successful nests, fledging success was higher ($\chi^2 = 17.7$, df = 1, $P < 0.001$) in culverts (94.5% vs 88.7%); this difference was consistent between years and was reflected in both hatching and nestling success. It appears, therefore, that while losses of complete clutches (broods), rather than partial losses, is the rule, this tendency is most pronounced in culvert nests. Partial losses appear more common in bridge nests, and thus, other losses must be correspondingly higher in culvert nests.

I found nesting success significantly lower ($\chi^2 = 7.5$, df = 1, $P < 0.01$) on creosoted wood than concrete bridges, 55.0% vs 78.8%. Jackson and Burchfield (1975) found that Barn Swallows (*Hirundo rustica*) rarely used creosoted wood bridges in Mississippi and speculated about noxious effects of creosote or increased susceptibility to predation. Because the increased losses I found on creosoted wood bridges were not from lowered hatchability or nestling survival, I do not think lowered success was attributable to any chemical characteristics of creosote. Wooden bridges have many structural support elements, e.g., braces, bolts, etc., to supply passage for predators and wood presents an easier climbing surface than concrete.

No information is available on post-fledging and adult survival in phoebes. If a population remains stable, however, and adult mortality is about average for temperate passerines, i.e., 50% (Ricklefs 1973), post-fledging juvenile mortality is high. A rough estimate of young fledged/pair may be obtained using the method of Nice (1937) and the conservative estimate of 2.18

attempts/pair: 1970—6.76 young/pair; 1971—5.14 young/pair; both years—5.97 young/pair. Therefore, the post-fledging survival required to balance adult losses would be 14.8% in 1970, 19.5% in 1971, and 16.7% overall. Since phoebes move north very early, they are periodically victims of spring storms. In such years, increased first-year survival could prevent a prolonged population depression.

Causes and stage of nest failures.—Causes of nest losses on Crane NWSC were varied, but no losses in the 2 years were attributed to human or livestock interferences. Almost half (49.3%) of the losses, constituting 18.2% of all attempts, was attributed to nest predators; 3 times as many losses were from predation as from the next leading factor. However, both the percentage of total nesting attempts lost to predators and the proportion of total losses attributed to predation were lower in these data than in many studies of nidicolous species. Nolan (1963) attributed 88% of all failures in deciduous shrub habitat to predation, while Lack (1954) thought that 75% of failures in open-nesting species were attributable to predation.

Since phoebe nesting success was generally higher than that for open-nesting altricial birds and the percentage of total losses attributed to predators was less, I conclude that nest-site selection by the Eastern Phoebe affords them a certain degree of security from predation. I believe the principal nest predators were the black rat snake (*Elaphe o. obsoleta*), raccoon (*Procyon lotor*), and white-footed mouse (*Peromyscus leucopus*). Because no House Wrens (*Troglodytes aedon*), House Sparrows (*Passer domesticus*), or Common Grackles (*Quiscalus quiscula*) nested on structures with phoebes, and since Blue Jays (*Cyanocitta cristata*) were never observed at bridges, I believe that avian nest predation was minor if it occurred at all.

Abandonment, always in the egg stage, accounted for over 15% of losses, but its cause was generally unknown. Losses from nests falling (12.7%) or from flooding (7.0%) were lower than expected. Various mites are common in phoebes and frequently infest young but in only 4 infestations was the parasite load sufficient to cause nestling death. In 3 of 11 instances of clutch abandonment, nests were heavily infested with mites, and the eggs were covered with dark stains from mite droppings. These large populations may have caused the abandonment.

Although cowbirds are common on Crane NWSC, only 7 phoebe nests (3.6% of all nesting attempts) failed from cowbird interference; 3 additional nests received at least 1 cowbird egg, but 2 of these were successful and the other was destroyed by a predator. This yields a parasitism frequency of 5.1%. Although it appears that cowbird interference in this phoebe population is light (Mayfield 1965), Friedmann (1963) identified the Eastern Phoebe as a very important cowbird host. In addition, Klaas (1975) found parasitism frequency of 24% in his study; and Graber et al. (1974), in central and southern Illinois with the exception of the extreme southern counties, found 30% of all nests affected. A more critical examination of my data revealed that 5 of 15 (33%) nests in natural locations received cowbird eggs while only 6 of 186 (3%) on artificial structures were parasitized. This difference is significant ($\chi^2 = 33.6$, df = 1, $P < 0.001$). Although Graber et al. (1974) gave no nest-site breakdown, their discussion suggested that a considerable number were in natural locations. Klaas (1975), on the other hand, examined only nests on bridges and culverts; on his study area there were no natural sites for nests. He stated that because it is an early breeder, the phoebe "receives most of the cowbird's attentions" early in the season. Although only a small number of nests in natural sites were examined on Crane NWSC, it appears that the same may be true for these nests in southern Indiana. Reduced cowbird parasitism alone could have been a significant selective factor in the substantial adoption of man-made structures as nest-sites, even in areas of plentiful natural sites.

Failure rate appeared higher for adherent than statant nests, but the apportionment of losses among the various causes was very similar. Five of the 7 losses to cowbird interference were of statant nests, reflecting the fact that most nests in natural sites were statant. The only rather substantial difference was higher abandonment of adherent nests (19.5% to 11.1%), possibly an indication that higher energy demands of adherent nest construction (Weeks 1978, Klaas 1970) lowers the energy reserves of females.

SUMMARY

Nesting ecology of Eastern Phoebes was examined in south-central Indiana in 1970 and 1971. The majority of the nests examined were on bridges and culverts.

Nest building began about 1 April, took 7–12 days, and completed nests stood empty for 1–9 days before egg-laying began. Both adherent and statant nests were built, the former being larger and apparently more energy demanding. Phoebes frequently used nests from previous years and reused the same nest (47.1% in 1970 and 51.5% in 1971) for a scond brood.

Nesting success in 1970 (70.3%) was significantly higher than in 1971 (57.3%), as was fledging success. Success changed little or declined slightly as the season advanced and varied according to nest-site.

Fledging success was highest in months when nesting intensity was highest. Fledging success was slightly higher in statant than adherent nests, but partial clutch (brood) losses were highest in statant nests. Similarly, success was somewhat higher on bridges than culverts, but probability of partial losses was greater on bridges. An average of 5.97 young/pair/year was fledged.

Predation was the major cause of nest failure with 49.3% of all losses, constituting 18.2% of all nest attempts, attributed to predation. Abandonment was the next leading cause, with Brown-headed Cowbird interference causing failure of only 3.6% of attempts. Cowbirds parasitized a significantly higher percent of nests in natural than artificial sites.

Nest losses were greatest in early egg or mid- to late nestling stages. Nest mortality rate was 0.97%/day. Mortality rate was higher for eggs (1.35%/day) than nestlings (0.91%/day).

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DEPT. OF FORESTRY AND NATURAL RESOURCES, PURDUE UNIV., WEST LAFAYETTE, INDIANA 47907. ACCEPTED 14 AUG. 1978.

RESOLUTIONS COMMITTEE

The Chairwoman of the Resolutions Committee for 1979–80 is Helen S. Lapham, Laboratory of Ornithology, Cornell University, Ithaca, New York 14850. Any member who knows of an issue upon which it would be appropriate for the Wilson Society to take an official position should communicate this information to Ms. Lapham before the annual meeting in March 1980. The resolutions adopted at each annual meeting are the only way in which the membership can unite to express, through the Society, a formal position on conservation matters.

Wilson Bull., 91(3), 1979, pp. 455–457

GENERAL NOTES

Age of effective homeothermy in nestling Tree Swallows according to brood size.—The development of thermoregulatory abilities in altricial nestlings has often been studied under laboratory conditions (Dunn, Condor 77:288–293, 1975), but rarely in nature. Dunn (Wilson Bull. 88:478–482, 1976) showed that large broods of House Wrens (*Troglodytes aedon*) in nest boxes with natural nests could thermoregulate effectively at half the age as could a single nestling. This note presents data collected in the same manner for nestling Tree Swallows (*Iridoprocne bicolor*).

Methods are described only briefly here; for full details see Dunn (1976). Nest boxes in Port Rowan, Norfolk Co., Ontario, were visited on cool mornings (15–25°C) in June 1977. Telethermometer probes were used to monitor ambient temperature (T_a) and air temperature inside the box. The latter was only once more than 4°C above T_a. Body temperatures (T_b) of the nestlings were measured with a small animal probe inserted into the gullet. I removed 1 nestling immediately upon my arrival at the box, measured its T_b, and quickly replaced it in the box. Different young (if possible), were removed at 5-min intervals for T_b measurement, until 20 min had passed. To determine age of physiological endothermy (the age at which a single nestling without insulation from parent, sibs or nest could thermoregulate; Dunn 1976), a single nestling was placed on a sheet of cardboard and protected from wind and direct sunlight. Measurements took place as described above.

Thermoregulatory performance was standardized by converting the difference between average T_a over the 20-min interval and T_b at each measurement to a percentage of the difference between average T_a and adult T_b (taken as 40°C). Thus, a nestling with a T_b of 25°C in an average T_a of 20°C showed 25% of adult thermoregulatory capacity. Age of effective homeothermy was arbitrarily defined as that age at which 75% of adult thermoregulation could be maintained after 20 min of exposure to a T_a of less than 25°C.

Fig. 1 shows the results of these measurements. My best estimate of the age and weight at which young Tree Swallows can thermoregulate effectively in various brood sizes, based on the data in Fig. 1, is given in Table 1.

The variability in the data was much greater for Tree Swallows than for House Wrens (Dunn 1976), perhaps due to a greater variability in the degree of nest insulation. Tree Swallows build a platform of dead grasses with a shallow cup, then line this with feathers. Linings ranged from 1 or 2 small feathers to luxurious cups of downy swan feathers curling over the young. House Wren nests were more uniform. In addition, a prolonged cold spell during the study period may have adversely affected the swallows' normal growth pattern.

The summary in Table 1 shows that in spite of greater variability, Tree Swallows have ages of effective homeothermy at each brood size very similar to those of House Wrens, even though adult swallows weigh about twice as much as House Wren adults. Growth rate *K*, a constant relating to the growth curve and representing the rate at which asymptotic weight is achieved (Ricklefs, Ibis 110:419–451, 1968), is 0.428 for Tree Swallows and 0.464 for House Wrens (Dunn 1975); and the age of physiological endothermy (endothermy of single nestlings under standard laboratory conditions) is about 9.5 days for both species. Overall developmental rate has been shown to be the best predictor of age of physiological endothermy (Dunn 1975), and the similarity of growth pattern of the 2 species, combined with their similarity of nesting situation, probably accounts for the closeness of ages of effective homeothermy in various brood sizes.

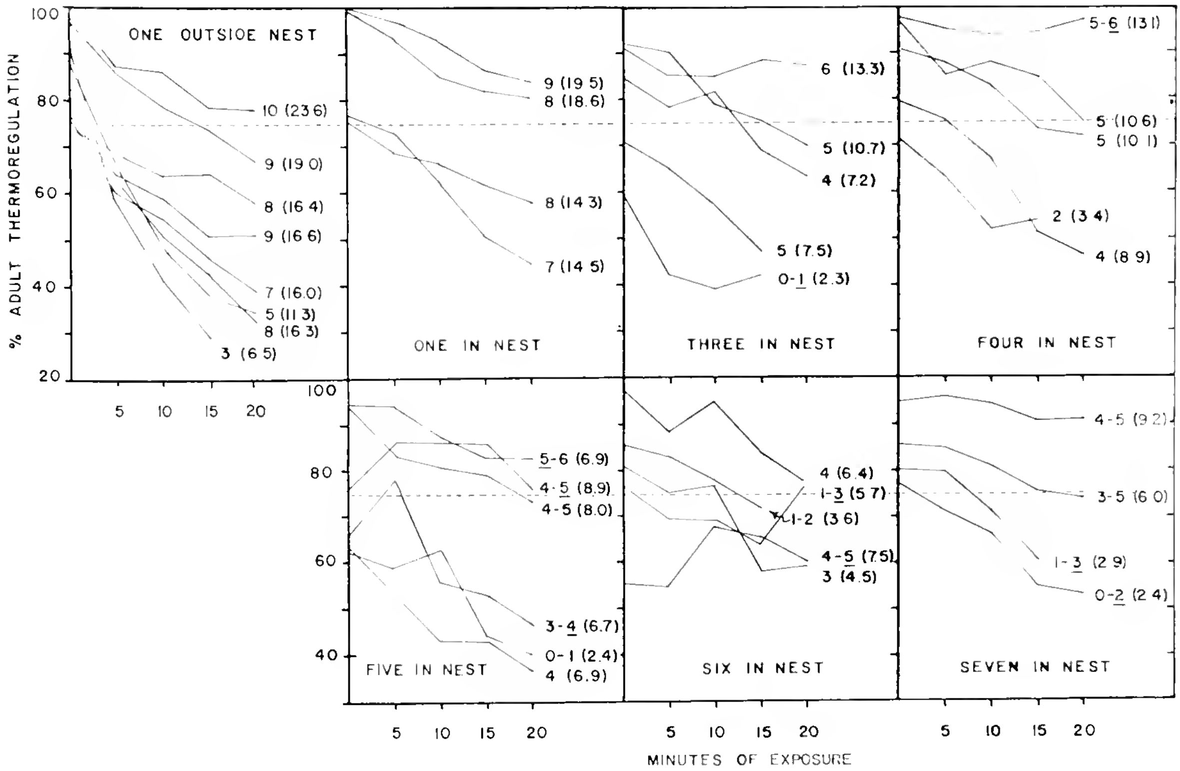

FIG. 1. Body temperatures of Tree Swallow nestlings after 5, 10, 15 and 20 min without parental brooding, expressed as percent of adult thermoregulation (see text). Each line represents 1 series of measurements on a brood. The age in days and average weight of nestlings (in parentheses) is given at the end of each cooling curve, with the predominant age underlined where appropriate. The dashed line shows level of effective homeothermy, defined as 75% of adult thermoregulation.

It is notable that Tree Swallows show a large drop in age of effective homeothermy in the nest once the brood size is larger than 1 (broods of 2 were not tested), but there is little change from small to large broods (Table 1). House Wrens, on the other hand, show a marked drop in age of effective homeothermy in broods of 4 and above. The difference probably results from different huddling behavior of the 2 species. Tree Swallows, even in broods of 7, sat next to each other in a single layer; while House Wrens nesting in

TABLE 1

AGE AND WEIGHT AT WHICH NESTLING TREE SWALLOWS CAN THERMOREGULATE EFFECTIVELY IN VARIOUS BROOD SIZES (SUMMARIZED FROM FIG. 1)

	Out of nest	Inside nest and nest box					
Brood size	1	1	3	4	5	6	7
Age (days)	9.5	8	6	5.5	5	4	4
Average weight (g)/nestling[a]	21–23	16–18	12–13	11–12	9	6	6

[a] Range of weights indicates that g/nestling at a given age varies from brood to brood.

similar-sized boxes made a single layer with 3 or fewer young, but a double layer in larger brood sizes. In both species, the average weight of nestlings at age of effective homeothermy can be less in larger broods, even though age of effective thermoregulation remains about the same. The difference in behavior and nest construction might affect thermoregulatory abilities in hot weather, but this has not been tested in either species.

I thank Trent University for the loan of telethermometers, and the Long Point Bird Observatory for the use of its facilities and access to the swallows.—ERICA H. DUNN, *Long Point Bird Observatory, P.O. Box 160, Port Rowan, Ontario, Canada N0E 1M0.* *Accepted 27 Sept. 1978.*

Wilson Bull., 91(3), 1979, pp. 457–461

The Oilbirds of Los Tayos.—A comprehensive investigation of the fauna of the Los Tayos caves (3° 06′ S, 78° 12′ W), in the Morana-Santiago Province of Ecuador, was one of the main objectives of the 1976 Ecuadorean-British Los Tayos Expedition. I studied the population of Oilbirds (*Steatornis caripensis*) inhabiting the caves.

The Los Tayos caves are situated in forested country at an elevation of 550 m in the eastern foothills of the Andes. The main entrances to the caves are 2 vertical shafts 55 m and 75 m deep and approximately 60 m apart. While the total cave system is large and complicated, with a surveyed length of 4900 m including several parallel systems, some with narrow exits, only the area within 200 m of the 2 main shafts was occupied by Oilbirds. The extent of the Oilbird's occupation was assessed by the position of the large deposits of seeds in the cave regurgitated by the birds after digestion of the pericarp.

Size of the Los Tayos colony.—The large size of the seed deposits, at least 2.5 m deep, indicated a long occupation by a large colony of Oilbirds, but relatively few of them (ca. 170) were in the caves during our visit. Indirect evidence of the probable size of the colony was obtained from local Indians. Traditionally these people harvest the young Oilbirds each year in April; in April 1976 they claim to have taken 500 young birds. A long-term investigation of the biology of the Oilbird in Trinidad (D. W. Snow, Zoologica 46:27–48, 1961; Zoologica 47:199–221, 1962) showed that on average a little over 2 young were reared per pair. If the nesting success at Los Tayos was similar then approximately 500 adults will have reared the 500 young birds killed. As many nesting ledges in the caves were very high and inaccessible to the Indians and annual harvesting of the young is a long cultural tradition, the proportion taken is likely to be a sustainable yield, indicating a total adult population of well over 500 birds, probably at least 1500.

On 14 July and 2 August between dusk and 21:00, I censused the Oilbirds as they left both vertical shafts of the cave to forage. On both evenings nearly all the Oilbirds left via the wider 75 m shaft. They negotiated the shaft singly using their echo-locating clicks as they circled upward. When they got out of the shaft they stopped echo-locating and flew into the forest. On 14 July 156 birds emerged and on 2 August 13 did so. On the former date after the main exodus a few adults could be heard still calling and clicking in the cave.

Breeding, and post-breeding exodus.—I entered the caves on 15, 20, and 24 July by means of a winch erected by the caving team. The occupied nesting ledges were all high and inaccessible, but from the cries of the young begging for food and from what I could view from below, I estimated that there were probably 10 to 15 nests with large young

TABLE 1

WING LENGTHS AND WEIGHTS OF YOUNG OILBIRDS

Estimated age (days)	Wing (mm)	Weight (g)	Average wt. and range at equivalent age in Trinidad
100[1]	279	281	485 (420–550)
80	200	196	600 (550–650)
80	244	165	600 (550–650)
60–70	125	228	520 (390–650)

[1] Fledged bird trapped in net.

on 15 July. By 24 July the cave appeared to be empty of Oilbirds except for 1 family of large young. During 4 July different young Oilbirds were picked up from the cave floor having fallen from the nests; all were emaciated. The weights and measurements of 3 of them, and of a fully fledged young bird caught on 7 July in a net 200 m from the shaft, are shown in Table 1.

Oilbirds in Trinidad take between 88 to 125 days to fledge; they reach a peak weight of ca. 650 g between 70 to 80 days, which then declines by approximately 200 g before fledging. Using the Trinidad data on wing length as a basis for estimating age, a comparison between the weights of the Los Tayos young and the young Trinidad birds is also shown in Table 1. The unfledged young were 56–72% below the weight of the Trinidad young and the fledged bird 42% below.

Between 7 and 25 July some members of the expedition were present in the Los Tayos caves each day but nobody actively disturbed the Oilbirds and it does not seem likely that human disturbance caused the exodus of most of the breeding population and the very low weights of the young.

If such a post-breeding exodus is normal it is in sharp contrast to the behavior of the Trinidad population which occupy their nesting ledges throughout the year. Huge numbers are also always present at the Caripe cave in Venezuela, now a national park and visited daily by tourists without disturbance to the birds.

Food.—The Oilbirds in Trinidad take their fruit almost entirely from 3 families and in the following proportions: Palmae 52%, Burseraceae 25%, and Lauraceae 23%. All these fruits have nonsucculent pericarps enclosing a single seed. Analysis of the pericarp of some fruits from each family showed them to be high in protein (9–14% dry wt.) and fat 24–44% dry wt.). Most of the fruits taken by the Oilbirds at Los Tayos were also from these 3 families (Table 2). The seeds of the fruits taken by the Oilbirds at Los Tayos that have not been previously illustrated in Snow (1962) are illustrated in Fig. 1 except for *Jessenia batana* whose seed appears identical to *Jessenia oligocarpa* of Trinidad. A sample of all the Oilbird seeds from the Los Tayos cave has been preserved and is deposited at the Sub-department of Ornithology of the British Museum (Nat. Hist.) at Tring.

Only 1 palm (*Morenia caudata*) was found with ripe fruit that could be collected for analysis. Twelve of these fruits weighed 53.5 g of which 35.5 g was seed and 16.5 g (31%) pericarp. The pericarp of the 12 fruits dried in the field weighed 3.0 g. Analysis of this dried pericarp showed it to be 11% fat; 9% protein; 70% carbohydrate, ash and crude

TABLE 2

PERCENTAGE PROPORTIONS OF OILBIRD FRUITS

	Random sample of seeds from top 30 cm of deposit	Freshly regurgitated seeds[1]		
		15 July	20 July	24 July
Burseraceae				
Dacryodes sp.	56	27	4	7
Palmae				
Jessenia bataua	3	–	2	–
Euterpe sp.	10	66	88	87
Morenia caudata	3	–	5	1
Socratea sp.	18	–	–	2
Lauraceae				
Aniba sp.	3	2	–	–
Small Lauraceae sp. (seed 15 × 9 mm)	2	–	–	–
Annonaceae sp.	4	–	–	½
Polygonaceae				
? *Coccoloba* sp.	2	4	1	2
Total seeds	460	48	193	187

[1] For sampling, I laid out a plastic sheet (183 × 274 cm) below some occupied ledges.

fibre; and 10% residual moisture. An analysis was made of the dried pericarp of 2 palm fruits taken by the Oilbirds in Trinidad; the results were *Bactris cuesa* protein 13%, fat 39%, *Jessenia oligocarpa* protein 5%, fat 26%, so both were considerably higher in fat than *Morenia caudata*.

Two methods were used to assess the fruit diet. A large random sample of seeds from the top 30 cm of the deposits was taken in the 2 largest colonies from dry areas. Some seeds, particularly the palms, are more durable than others so may be slightly over represented by this sampling method. Recently regurgitated seeds were also sampled. Before laying out a plastic sheet on 15 July to sample recently regurgitated seeds, the fresh seeds on the surface, identifiable by the pink or purplish stain made by the recently enclosing pericarp, were collected. A general search of the cave deposits did not produce any more kinds of seeds than were taken in the samples.

During the short span of observations the changes in the birds' diet suggested a food shortage. There was a decrease in the proportion of *Dacryodes*, a large fruit with a seed size averaging 26 × 17 × 16 mm; while the proportion of the palm *Euterpe* was high throughout July and increased in the second half. *Euterpe* has a round seed that varies in diameter from 9–16 mm (average of 12 seeds 13 mm) and is the smallest fruit taken by the Oilbirds at Los Tayos. The fresh *Euterpe* seeds collected were nearly all below average: of the 32 seeds collected on 15 July the largest was 11 mm; of the 147 seeds collected on 20 July all but 3 were under 12 mm; and of 125 seeds collected on 24 July all but 1 was under 11 mm.

The most striking difference between the Oilbird's diet in Trinidad and Los Tayos is

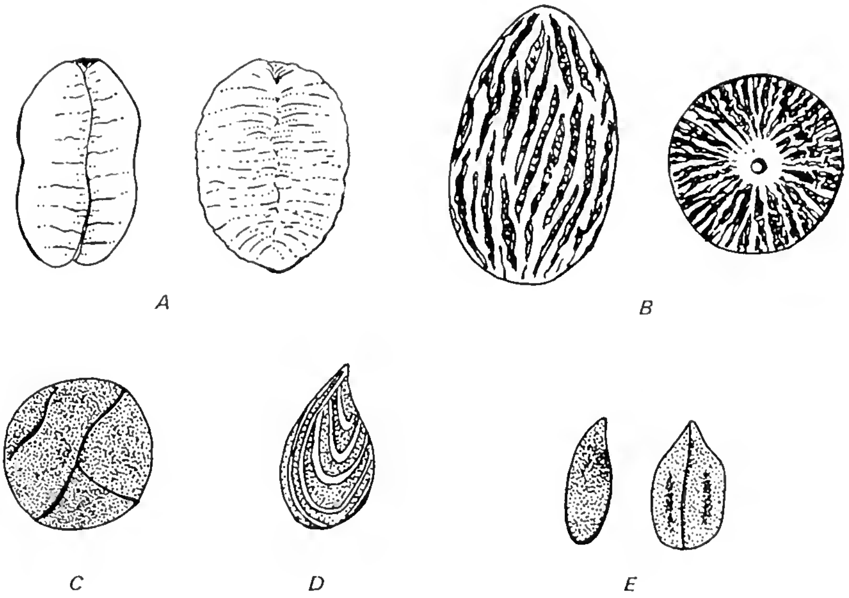

FIG. 1. Seeds of fruits eaten by Oilbirds. Natural size. A. Annonaceae sp., color reddish brown. B. *Socratea* sp., color reddish brown with black streaks. C. *Morenia caudata*, color black, indented lines. D. ?*Coccoloba* sp., color brown or black with raised fibres. E. Lauraceae sp., color dark brown.

the paucity of Lauraceae at Los Tayos. Two species of Lauraceae account for 5% of the large random sample taken at Los Tayos, compared to 15 species of Lauraceae accounting for 23% of all seed samples taken in Trinidad.

Yaupi caves, 33 km ENE of Los Tayos caves, were visited by some members of the expedition between 26 and 31 July. No Oilbirds were found in the caves but there were deposits of Oilbird seeds. The local Indians claim that Oilbirds breed there and they harvest the young in March and April. A. Hutson kindly collected a small sample of the seeds, picking out as many different kinds as he could find. This sample includes all the palm species shown in Table 2 but only 2 dicotyledon species, the Annonaceae species, and an unidentified species not found at Los Tayos. The absence of *Dacryodes* and of the Lauraceae is not surprising as Yaupi caves are below 275 m, where the Rio Santiago has left the mountains, and *Dacryodes* is a mountain species as are most of the Lauraceae.

Comparison between Los Tayos and Trinidad colonies.—The Oilbird colony studied at Spring Hill in Trinidad was a small one of 25 to 30 birds in a small partially roofed gorge and the size of the colony was almost certainly controlled by the number of suitable nesting ledges. Since the study was made the addition of a few artificial ledges has slightly increased the size of the colony. The cave is surrounded by rich forest and the nearest neighboring Oilbird cave is 8 km away. Throughout the 4½ years of the Trinidad study there was no indication of food shortage. The year-round occupation of nesting ledges here may be necessary to ensure the opportunity to breed.

At Los Tayos on the other hand, the colony size is probably not limited by available nesting ledges as much of the cave system is not used; therefore year-round occupation might serve no function. Colony size is possibly limited by the fruit available within the energetically economic foraging distance from the cave. If this is so it would not be surprising that at the end of the breeding season the young should be very much underweight or that the adults desert the cave at this time.

Acknowledgments.—I should like to thank the members of the joint Ecuadorean-British expedition for their help, particularly the caving team who made entry to the cave possible. I also thank the Los Tayos Expedition 1976 Trust for their logistic and financial support and A. Hutson and Dr. C. de Vries for assistance with field observations. I am also indebted to Dr. H. E. Moore for identifying some of the palms.—BARBARA K. SNOW, *Old Forge, Wingrave, Nr. Aylesbury, Bucks., England.* *Accepted 14 Aug. 1978.*

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Observations on the nesting biology of the Great Cormorant in Ethiopia.—The breeding biology of the Great Cormorant (*Phalacrocorax carbo*) is fairly well known for northern temperate populations (Cramp and Simmons, Birds of the Western Palearctic Vol. I, Oxford University Press. Oxford, 1977; Palmer, Handbook of North American Birds Vol. I, Yale University Press, New Haven, 1962) but not for African populations (Olver and Kuyper, Ostrich 49:25–30, 1978; Urban and Jefford, Emu 74 [Suppl.]: 294, 1975). This paper, one in a series on the breeding biology of large water birds nesting in the Rift Valley of Ethiopia, presents observations on breeding plumage, pair formation, nest building, incubation, and behavior, care and predators of nestlings of *P. c. lucidus.*

Study area and methods.—Observations were made at Lake Shala (7° 30′ N, 38° 30′ E; 330 km^2; max. depth 266 m; pH 10.0) and Lake Abiata (7° 35′ N, 38° 35′ E; 196 km^2; max. depth 14 m; pH 10.3) (Urban, Ibis 116:263–277, 1974). Throughout the period of observation from 1964–1974, the Great Cormorant nested at Shala on trees on islands, although in 1969–1974 they also nested at Abiata in trees surrounded by water due to a substantial rise in the lake's level. Observations, made usually once a month on weekends, totalled 240 h in 87 visits to Shala and 110 h in 56 visits to Abiata. The birds were observed from at least 20 m away in a boat or on the ground. No blind was used nor were any nestlings or adults banded or marked. Classification of *carbo* used in this paper is from Urban and Jefford (Bull. Br. Ornithol. Club 94:104–107, 1974); names of colors are from Palmer (op. cit.); and names of displays are from van Tets (Ornithol. Monogr. 2, 1965).

Breeding plumage.—The lores—orange in male and scarlet, scarlet-orange, or orange in the female early in the nesting cycle—turn orange-yellow in both sexes once incubation begins. The breeding plumage is otherwise essentially the same in both adult sexes: the cheeks, throat, and upper breast are white while the rest of the body is black glossed with olive. The lower breast and abdomen are speckled white and black in immatures (2- to 3-year-olds ?) and white in 1-year-olds. An oval white patch is often present (adults only ?) on either side of the rump in both sexes, not only in males as stated by Olver and Kuyper (op. cit.). The gular pouch, olive to dark olive early in the breeding season, becomes olive to buffy yellow in late stages of incubation. The iris is emerald.

Pair formation.—Nesting activity commences when a few to several hundred cormorants appear at the islands at Shala or on the partly submerged trees at Abiata. Occasionally 300 or more individuals swim in a group close to the islands of Shala for several h before moving onto them. Pair formation at Shala and Abiata appears to be much like pair formation in *carbo* populations in northern temperate regions as described by Cramp and Simmons (op. cit.). Thus, males establish nest-sites and advertise on them by wing-waving; they are silent when doing so. Based on 30 observations, the males waved the wings 1.8 times per sec and 11 times in a sequence before stopping. European and North American *carbo* males do so 1.3–1.7 times per sec and 8–25 times before stopping (van Tets, op. cit.). When approached by a female, a male shifts from wing waving to gaping and produces a loud *a/rrooo* or *a/a/a/a/rrooo.* The female responds by placing the head and bill halfway back to the tail, not all the way back to it as the male does, and by producing a soft *hrrr.* Both also point, allopreen, and entwine the necks. If the female remains at the nest, the male will collect nesting material which he gives her upon his return.

Early in the nesting cycle, both sexes produce 1 to 2 "growls" before departing the nest. Later in the nesting season both sexes are silent when leaving the nest. When returning to the nest-site early in the nesting season, the female produces a soft *hhhhhhhhhh* while the male makes a loud *kro/kro/kro/kroo/kroa/kraa.* Later in the nesting season, both only produce a *kro/kro/kro/kro* similar to but not so loud as that produced earlier by the male. These changes in vocalizations have also been observed by Kortlandt (Arch. Ne'erl. Zool. 4:403–422, 1940; and pers. comm.) in Dutch *carbo* populations.

No distinctive pre- or post-copulatory displays occur. At copulation the female flattens her body with bill pointed forward; and the male may nibble the back of her neck. Three timed copulations (success ?) lasted 1, 2, and 7 sec.

No display platforms, as Kortlandt (loc. cit.) described, were observed at the Shala and Abiata colonies. Occasionally 1- to 2-year-old individuals wing-waved, gaped, or pointed on tree stumps or branches projecting out of the water at Abiata.

Nest building.—Once pair formation is established, the pair builds the nest with the male typically collecting the material, and the female constructing the nest. At Shala the males collected nest material mainly from the islands; at Abiata they collected the material from trees and other partly-submerged vegetation close to the colony. Males regularly took material from unguarded or abandoned nests. Nests varied from touching each other to being several m apart and from 0.5–5 m above the water level at Abiata or the ground at Shala. Most nests contained unidentified sticks, 0.5–1.5 × 10–40 cm in size, interspaced with grass (*Sporobolus* sp.) and unidentified feathers. Most were lined with the grass and feathers, although occasionally a nest consisted of only grass and feathers. Several unoccupied nests at Abiata contained innumerable unidentified small mites, each about 0.5 mm long. The dimensions of 25 nests measured at Abiata were: outside rim 47 × 50 cm–33 × 35 cm (av. 39.5 × 39.4 cm), inside rim 28 × 30 cm–21 × 21 cm (av. 24.0 × 23.6 cm), depth central depression 1.0–6.5 cm (av. 3.9 cm), and thickness from top to bottom 13–27 cm (av. 20.3 cm). Occasionally other nests at Abiata were 1 m thick from top to bottom.

Incubation.—Clutch-size, based on 96 nests, averaged 2.24 eggs. Since siblings from the same nests were usually the same size, incubation probably begins when the clutch is complete. However, on occasion one of a brood was smaller in size, indicating that incubation also starts before the clutch is complete. Incubation, done by both parents, lasted about 28–29 days. During the first few days of incubation, the parent (sex ?) sitting on the nest angles the tail about 45° above the horizontal axis; the significance of this behavior, which appears not to have been reported previously, was not determined.

Behavior of young.—Nestlings, from time of hatching to about 2-weeks of age, appear to be active only when the parents feed them. When the nestling is about 4-weeks-old, it is active, jabbing at neighbors or siblings, but it normally does not leave the nest. Sometimes during the heat of the day, the 4-week-old nestling hangs the head and neck over the shady side of the nest. When it is about 5–6 weeks old, the nestling flaps the wings during wind and rain storms and occasionally flies a few meters. At this age, it moves sticks in the nest and gapes much like an adult female does. When the nestling is about 8-weeks-old, it flies nearly as well as the adult although it takes about twice as long as the adult to rise from the surface of the water.

Care of young.—Both parents usually are at the nest at time of hatching. At least 1 parent is at the nest from time of hatching until the nestling is about 1–2 weeks old. Thereafter, the parents come and go until, when the nestling is about 6-weeks old, a parent is at the nest only at feeding time. Both parents, nevertheless, appear to care for the young birds until they are about 8-weeks-old; no adult was seen carrying for any older young.

The very small young cormorants seem to be fed at regular intervals throughout the day, and each feeding sequence may last 45 min. Nestlings 3-weeks-old and older seem to be fed once every 24 h, most often 1 to 2 h before sunset but not uncommonly shortly after sunrise and at mid-day. Normally, feeding of young 3-weeks-old and older does not last long. Thus, 42 feeds by 6-weeks-old young ranged between 3.8 and 17.8 sec (av. 8.8 sec). However, the young bird may be fed at frequent intervals (one 3-week-old fed 7 times within ½ h with each feeding lasting about 10 sec) or the parent may remain with the young bird for several hours before feeding it (1 adult arrived at the nest but waited 2½ h before feeding a 4-week-old who begged during most of the period; another adult remained with a 4-week-old bird from 09:00–17:45, feeding it once at 15:30). During the warm mid-day temperatures, the parents fetch and give the nestlings water; this behavior will be described elsewhere.

The young birds remain close to the nest-site apparently awaiting the return of the adults. The nestling appears to recognize its parents; the adults seem to recognize and feed only their young. The young bird may fly or swim after an adult (its parent ?) when begging for food. When returning to the nest, the adult normally lands close to it. If the nestling is some distance from the nest, the parent does not appear to seek it out and eventually leaves the area without feeding it.

Parents seem to feed the most active and strongest siblings. A young bird, hatched later than its siblings, normally expires before reaching 2- to 3-weeks of age, due apparently to starvation or to accidentally being pushed out of the nest by its larger siblings. Young birds falling out of the nest in this manner and jumping out to avoid predators appear to be major causes of mortality at the colonies.

Predators.—Predators at the Shala and Abiata colonies include Marabous (*Leptoptilos crumeniferus*) taking eggs, nestlings and young cormorants nearly ready to fly; African Fish Eagles (*Haliaeetus vocifer*) who take eggs and nestlings to at least 3-weeks-old; and Black Kites (*Milvus migrans*) and Fan-tailed Ravens (*Corvus rhipidurus*) taking eggs and newly-hatched young. Egyptian Vultures (*Neophron percnopterus*) are uncommon at the colonies. Tawny Eagles (*Aquila rapax*), Marsh Harriers (*Circus aeruginosus*), Peregrine Falcons (*Falco peregrinus*), and other unidentified falcons were seen around the colonies but were not seen feeding on cormorant eggs or nestlings.

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American Woodcock hatched in Alabama killed in Michigan.—Since the winter of 1973–74 researchers at Auburn University have located numerous nests and broods of American Woodcock (*Philohela minor*) in Alabama between January and April. When possible, the females and their broods were leg-banded to try to gain information about dispersal of these southern nesters and their offspring.

In late winter and early spring of 1976 we located 35 broods and nests and banded 49 chicks and 11 females in various regions of Alabama. On 3 March 1976, a day-old brood of 4 chicks was banded on Wheeler National Wildlife Refuge near Decatur, Alabama.

On 1 October 1976, 1 young woodcock from this brood was killed by a hunter in Midland County, Michigan, approximately 650 air miles north of the banding site. The band recovery was verified by the U.S. Fish and Wildlife Service's Bird Banding Laboratory.

This is a very unusual recovery and raises new questions about the biology of the woodcock. Do these females and their broods move toward the more traditional breeding grounds as soon as the chicks are capable of sustained flight? Might these females also produce second broods on the northern breeding grounds? A coordinated effort by researchers in the other southern states to band chicks and females on the wintering grounds is needed to answer these questions.

This study was supported with funds from Federal Aid in Sport Fish and Wildlife Restoration through the Alabama Department of Conservation, Division of Game and Fish and by the Auburn University Agricultural Experiment Station.—KEITH CAUSEY, GEORGE HORTON, JOHN ROBOSKI, RANDALL JOHNSON, AND PHILLIP MASON, *Department of Zoology-Entomology, Auburn University Agricultural Experiment Station, Auburn, Alabama 36830.* *Accepted 24 June 1978.*

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Growth and age determination of nestling Brown-headed Cowbirds.—The purpose of this study was to determine daily growth of body parts and feather tracts of nestling Brown-headed Cowbirds (*Molothrus ater*). The study was conducted in Wood and Ottawa counties in northwestern Ohio during May and June 1975. Body parts and feather tracts studied are defined by Holcomb and Twiest (Wilson Bull. 82:294–303. 1970).

Each nest containing a cowbird egg or nestling was visited daily ±1 h of the last visit. Data were recorded only from nestlings that were first discovered as eggs. The day a nestling was first discovered to have hatched was considered day 1 for that bird; however, it is possible that a cowbird hatched after the daily visit and was actually some fraction of a day older than estimated. Body weight was measured to the nearest g using a Pesola Scale. Linear measurements were recorded to the nearest mm using dividers and a 15-cm ruler.

Twenty-three cowbird eggs were located in 17 nests from 16 May 1975 to 16 June 1975. Nine eggs hatched; the earliest hatching was 20 May and the latest hatching was 18 June. Five nestlings fledged, 3 at 10 days of age and 2 at 11 days of age.

Cowbird eggs were found in the nests of Yellow Warblers (*Dendroica petechia*), Red-winged Blackbirds (*Agelaius phoeniceus*), Cardinals (*Cardinalis cardinalis*), Indigo Buntings (*Passerina cyanea*), a Field Sparrow (*Spizella pusilla*), and Song Sparrows (*Melospiza melodia*). Cowbirds fledged from Yellow Warbler, Red-winged Blackbird, and Song Sparrow nests.

Means and SD of nestling cowbird measurements are presented in Table 1. All nestlings included in Table 1 either fledged or, presumably, were removed from the nest by predators. One nestling continued to lose weight from day 6 to day 10; on day 10 it died in the host Red-winged Blackbird's nest. This nestling was not included in the calculations for Table 1.

TABLE 1

THE $\bar{x} \pm$ SD INSTANTANEOUS DAILY GROWTH OF NESTLING BROWN-HEADED COWBIRDS

	Age and weight (g)										
Age (days)	1	2	3	4	5	6	7	8	9	10	11
Sample size	8	8	7	5	5	5	5	5	5	5	2
Weight	3 ± 1	5 ± 2	7 ± 2	12 ± 2	16 ± 1	20 ± 1	23 ± 1	25 ± 2	26 ± 2	28 ± 1	29 ± 1
	Body part measurements (mm)										
Total body length	39 ± 2	45 ± 4	53 ± 4	60 ± 3	67 ± 4	73 ± 2	80 ± 2	85 ± 4	94 ± 2	102 ± 2	108 ± 2
Tarsus	6 ± 1	7 ± 1	10 ± 1	13 ± 2	16 ± 1	17 ± 1	20 ± 1	22 ± 1	23 ± 1	24 ± 1	24 ± 0
Wing	8 ± 1	9 ± 1	12 ± 2	18 ± 4	27 ± 4	33 ± 4	40 ± 4	48 ± 4	52 ± 2	57 ± 2	64 ± 1
	Feather tract measurements (mm) and development[1,2,3]										
Caudal	N	N	N	N	P1 ± 1	P2 ± 1	P4 ± 1	F7 ± 2	F10 ± 2	F13 ± 2	F16 ± 1
Alar	N	N	P1 ± 1	P4 ± 1	P8 ± 2	P13 ± 2	F17 ± 3	F21 ± 3	F26 ± 3	F29 ± 2	F32 ± 1
Humeral	N	N	N	P2 ± 1	P3 ± 2	P6 ± 1	F9 ± 2	F11 ± 2	F13 ± 2	F16 ± 1	F19 ± 1
Capital	N	N	N	N	N	P1 ± 1	P3 ± 1	P4 ± 1	F5 ± 1	F6 ± 0	F7 ± 1
Spinal	N	N	N	N	P2 ± 1	P5 ± 2	F7 ± 2	F10 ± 1	F12 ± 1	F15 ± 2	F18 ± 1
Ventral				P1 ± 1	P2 ± 1	P4 ± 1	F6 ± 1	F9 ± 1	F11 ± 2	F15 ± 3	F16 ± 4
Crural	N	N	N	N	P1 ± 0	P2 ± 1	F4 ± 1	F5 ± 1	F6 ± 1	F7 ± 2	F8 ± 1
Femoral	N	N	N	N	P2 ± 1	P4 ± 1	F6 ± 1	F8 ± 1	F11 ± 1	F13 ± 1	F16 ± 1

[1] N = presence of neossoptiles.

[2] P = projection of teleoptile feather sheaths through the epidermis.

[3] F = fringing of teleoptile feather barbs from feather sheaths.

The mean weight of day 1 nestling cowbirds was 3 g, and the mean fledging weight was 28 g (Table 1). Weights presented in Table 1 are supported by Nice (Auk 47:419–420, 1930) who stated that on day 8 a cowbird raised by Song Sparrows weighed 24.5 g. Weight, however, probably varies more than other characters as environmental conditions vary and/or as different host species are parasitized; therefore, it should not be emphasized during age determination.

One nestling that was weighed within 30 min of hatching weighed 2.5 g. This weight agrees with Wetherbee and Wetherbee (Bird-Banding 32:141–159, 1961) who reported that 9 newly hatched cowbirds ranged in weight from 1.85 to 2.68 g ($\bar{x} = 2.22$ g).

Nestlings partially opened their eyes on day 4. No record was kept of when eyes were completely open.

Total body length and wing length are good body parts for age determination due to their rapid growth (Table 1). Gape reached a maximum width of 15 mm on day 5 and was maintained until day 8 when gape had declined to 14 mm, a width that was maintained until fledging. Mandible tip to nostril opening reached maximum length of 7 mm at day 10. All other body parts, including toe span and mandibular tomium, grew continuously from hatching to fledging.

Some nestling cowbirds lacked neossoptiles on their ventral tracts (6 of 9) and crural tracts (4 of 9). Neossoptiles were present on all other feather tracts examined. These results agree with reports cited by Wetherbee (Bull. Amer. Mus. Nat. History 113:339–436, 1957).

Due to early projection of feather sheaths through the epidermis, early fringing of feather barbs from feather sheaths, and rapid growth, the alar tract is the best feather tract for age determination (Table 1). The alar tract was the first to project (on day 3) and the capital tract was the last (on day 6). On day 7 all tracts except the caudal and capital tracts had fringed. All tracts were fringed by day 9 supporting Neal's (Condor 75:351–352, 1973) assertion that cowbirds are entirely homeothermic by day 10.

Researchers determining age of large numbers of nestling cowbirds should find total body length the best single character for age determination. Wing length and alar tract measurements are also useful for rapid age determination; however, these measurements are of little value during days 1 and 2. Thus, total body length must be measured during days 1 and 2 to accurately determine a nestling cowbird's age.

Sources of possible error should be mentioned. Nests in Ottawa County were visited from 07:00 to 11:00 while those in Wood County were inspected from 13:00 to 17:00. Differences in the time of day when data were recorded may have influenced results since nestlings grow rapidly. For example, if 2 nestlings (1 in each county) hatched at an identical time, their measurements would probably differ if one was measured at 07:00 and the other at 17:00. In addition, the sample size was small and nestlings raised by different hosts were pooled together. With a larger sample size it would be interesting to determine if cowbirds develop differently when raised by various hosts, especially if the comparison included cowbird nestlings raised by a common vs an uncommon host.

I wish to thank William B. Jackson for valuable suggestions that improved the initial manuscript. Larry C. Holcomb and P. Weatherhead provided helpful criticism of a later draft. Beth Clinger and Randy Strait assisted in the field by locating nests and recording growth data. Without the aid of Judith M. Grumstrup this writing would not be in its present form.—THOMAS W. SCOTT, *Environmental Studies Center, Bowling Green State Univ., Bowling Green, Ohio 43402 (Present address: Veterinary Science Dept., Pennsylvania State Univ., University Park, Pennsylvania 16802).* *Accepted 14 Aug. 1978.*

Wilson Bull., 91(3), 1979, pp. 467–468

Ground Dove use of young pine plantations.—Nesting and feeding habits of the Ground Dove (*Columbina passerina*) have been studied extensively in the lower Coastal Plain of the southeastern United States. Nesting has been recorded on the ground (Hopkins, Oriole 23:5–7, 1958), and in hardwood trees or shrubs, especially evergreens such as citrus trees (Nicholson, Wilson Bull. 49:101–114, 1937) and wax myrtle (*Myrica cerifera*) (Sprunt and Chamberlain, South Carolina Bird Life, Univ. South Carolina Press, Columbia, 1970). Most workers describe feeding habitat as thinly vegetated fields with some bare ground, in sandy, drier areas.

On 3 November 1977, we found 3 occupied Ground Dove nests in a 5-year-old slash pine (*Pinus elliottii*) plantation in Decatur County, Georgia. On 7 November, flushing counts were made along 4 transect lines, and each flushing site and each tree (planted and voluntary species) were examined for nests. Eight Ground Doves were collected for food habits analysis.

Seven active nests were located, 3 with a clutch of 2 eggs each, and 4 with 2 nestlings each. Nests were 0.4–1.5 m above ground on pine limbs containing witches'-brooms and fusiform rust (*Cronartium fusiforme*) cankers. No nests were found on the ground, or in oaks (*Quercus* spp.) or crabapple (*Malus angustifolia*), which composed 18% of the trees in the stand. The nests were sturdy, with a substrate of pine needles and oak and blackberry (*Rubus* spp.) twigs. The bowl-like interiors were composed of interwoven rootlets and grasses. They probably were refurbished nests built earlier by other species (see Nicholson, op. cit.). Young in all 7 nests were successfully reared to the fledgling stage; the last pair left the nest on 12 December. In a 0.7-ha portion of the stand, there was a density of 10 active nests per ha, and 36 volant Ground Doves (51/ha). Our findings represent the latest nesting dates recorded in Georgia and possibly the Southeast. Since active nests have been located as early as 23 January (Hopkins, op. cit.), this species may nest year-round.

TABLE 1

FOODS OF 8[a] EASTERN GROUND DOVES FROM DECATUR COUNTY, GEORGIA, 1977

Item	November		December	
	Occurrence	Volume (%)	Occurrence	Volume (%)
Three-seeded mercury (*Acalypha virginica*)	4	95.9	3	27.8
Croton (*Croton glandulosus*)	3	3.0	2	4.3
Yellow wood sorrel (*Oxalis stricta*)	3	1.0	2	tr[b]
Eyebane (*Euphorbia maculata*)	1	0.1	2	15.5
Texas panicum (*Panicum texanum*)	–	—	3	18.5
Marsh elder (*Iva annua*)	1	tr	1	17.3
Amaranth (*Amaranthus* spp.)	–	—	4	14.5
Ragweed (*Ambrosia artemisiifolia*)	1	tr	1	1.3
Panic grass (*Panicum dichotomiflorum*)	3	tr	2	0.5
Bull grass (*Paspalum boscianum*)	–	—	2	0.3

[a] Four were collected each month during November and December.

[b] tr indicates trace amounts <0.1% volume.

Most birds were seen in crabapple thickets and all but 4 were in areas with an understory of blackberry and scrub oaks. Birds were often seen feeding on the ground in small clearings with sparse herbaceous cover, especially in a 1-year-old plantation adjacent to the nesting area. The major food item (Table 1) was three-seeded mercury (*Acalypha virginica*), an important food in young pine stands in the Piedmont region (Landers et al., Oriole 42:10–12, 1977). This plant flourishes in areas of disturbance associated with tree planting or agricultural practices where little or no herbicides are applied.

Seedling pine stands with patchy herbaceous cover provide a variety of desirable small seeds for food. The sapling stage plantations, if interspersed with bushy thickets and sparse ground-level vegetation, can provide favorable sites for nesting and roosting for Ground Doves and other species.—J. LARRY LANDERS AND JAMES L. BUCKNER, *International Paper Company, Southlands Experiment Forest, Bainbridge, Georgia 31717. Accepted 7 Sept. 1978.*

Wilson Bull., 91(3), 1979, pp. 468–469

Loggerhead Shrike eggshell thickness in California and Florida.—Eggshell thinning has been documented in numerous birds of prey. Magnification of pesticide residues through the food chain of these species is likely responsible for alterations in shell structure (Anderson and Hickey, Proc. 15th Int. Ornithol. Congr., 514–540, 1972; Cooke, Environ. Pollution, 4:85–152, 1973). Loggerhead Shrikes (*Lanius ludovicianus*) prey on invertebrates and small vertebrates (Bent, U.S. Natl. Mus. Bull. 197, 1950), and thus may be susceptible to residue buildup through their diet as reflected by eggshell thickness.

All eggs measured were at the Western Foundation of Vertebrate Zoology. Eggs collected in California (1948–1976) and Florida (1950–1968) were compared to eggs collected prior to 1947 (pre-DDT). The length and breadth of blown eggs were measured (nearest 0.01 mm) with dial vernier calipers and weighed (nearest 0.001 g) on a Mettler P 120 balance. A "shell thickness index" (Ratcliffe, Nature, 215:208–210, 1967) was calculated for all eggs. All post-1947 indices were combined as results did not vary between decades. Data on pesticide content of shrike eggs were not available.

Little difference was found in shell indices between pre- and post-DDT Loggerhead Shrike eggs (Table 1). The minor change in the California sample was likely attributable to observer error and/or sample size. About 28 clutches of Loggerhead Shrike eggs must

TABLE 1

THICKNESS INDICES OF LOGGERHEAD SHRIKE EGGS

Locality	Mean thickness index ± SE (mm)		Percent change
	Pre-1947	Post-1947	
California	0.52 ± 0.004 (20/113)[a]	0.53 ± 0.005 (29/157)	+1.92[b]
Florida	0.52 ± 0.005 (17/81)	0.52 ± 0.006 (14/66)	—

[a] Total number of clutches/total number of eggs within clutches.
[b] $P > 0.05$, df = 47, *t*-test.

be measured to detect differences of 5% in shell thickness (Klaas et al., Wilson Bull. 86:156–164, 1974). Klaas et al. (op. cit.) calculated a thickness index of 0.515 for shrike eggs collected in Florida (N = 73 clutches) prior to 1943, which was nearly identical to indices calculated in this study.

The diet of shrikes is usually less than 30% vertebrates (Miller, Univ. Calif. Publ. Zool. 38:11–242, 1931). Pesticide accumulation may have been insufficient to cause eggshell thinning in shrikes. However, pesticides can cause reproductive failures even in the absence of shell thinning (Fox, Wilson Bull. 88:459–477, 1976). Although stable in the western United States, shrike populations are declining over much of the remainder of their range (Arbib, Am. Birds 31:1087–1097, 1977). Studies on the effects of low dietary pesticide levels on the viability of shrike eggs would be useful.

I wish to thank C. E. Grue, C. A. Campbell, and E. E. Klaas for reviewing the manuscript. Financial support during the study was granted by the Western Foundation of Vertebrate Zoology.—Michael L. Morrison, *Western Foundation of Vertebrate Zoology, 1100 Glendon Ave., Los Angeles, California 90024.* (Present address): *Dept. Fisheries and Wildlife, Oregon State Univ., Corvalis, Oregon 97331.)* *Accepted 19 Sept. 1978.*

Wilson Bull., 91(3), 1979, pp. 469–470

First sight records of Lincoln's Sparrow for Costa Rica.—Lincoln's Sparrow (*Melospiza lincolnii*) has been recorded south to El Salvador and Honduras; there are also 2 records (including a specimen) for Panamá (A.O.U., Check-list of North American Birds, Baltimore, 1957; Ridgely, Guide to the Birds of Panama, Princeton, 1976). Therefore, Costa Rica and Nicaragua constitute a hiatus in the species' known winter range. While studying North American migrants at Monteverde on the Pacific slope of the Cordillera de Tilarán, northwestern Costa Rica (10° 18′ N, 84° 49′ W) during the winter of 1976–77, I observed a single Lincoln's Sparrow on 3 occasions. On 9 January, I "spished up" a bird from dense tall grass on a hillside. On 17 February, Thomas Kemp, Marcie Lawton and I saw another (?) bird fly up from dense grass into a low shrub on a steep hillside. Spishing also brought this bird into clear view several times. Finally, on 20 February I saw a Lincoln's Sparrow at close range in short dense grasses and malvaceous forbs along a roadside. All these locations are less than 1 km apart and between 1390 and 1440 m elevation near the center of the Monteverde community, so it is possible that all 3 observations represented a single individual.

Each time the bird was observed in full sunlight through 8× binoculars. In both markings and actions, the birds were typical of the many Lincoln's Sparrows I have seen in North America except the buffy breast band was not evident (Lincoln's Sparrows occasionally lack this feature). The only other sparrow-like finch at Monteverde is the resident Rufous-collared Sparrow (*Zonotrichia capensis*), of which I saw many each day. Immature *Z. capensis* bear a superficial resemblance to *Melospiza* sparrows. During January–February very few *Z. capensis* were in the immature plumage; I saw only 2 such birds during my stay. Both were easily recognizable by their uneven upper breast streaking (heaviest on the sides of the neck), noticeably white throat, no eyering or malar stripe, the beginnings of a rufous nape patch, noticeably notched tail, and more stocky shape than *Melospiza lincolnii*. Rufous-collared Sparrows rarely used the overgrown habitats where Lincoln's Sparrows were found; rather, they preferred the vicinity of fencerows or clumps of small trees in open, close-cropped pastures.

I suspect that a search of abandoned fields and pastures in the Costa Rican highlands will yield additional sight records of Lincoln's Sparrow and a first Costa Rican specimen. Unfortunately, it was not possible to capture or photograph these birds. I thank F. Gary Stiles and Eugene Eisenmann for commenting on this manuscript. I also gratefully acknowledge the support of National Science Foundation grant #DEB76-10787.—ELLIOT J. TRAMER, *Department of Biology, The University of Toledo, Toledo, Ohio 43606.* *Accepted 4 Sept. 1978.*

Wilson Bull., 91(3), 1979, p. 470

An incident of Blue Jay predation on a House Sparrow.—Few instances of Blue Jay (*Cyanocitta cristata*) predation on other, mature birds have been documented. Johnson and Johnson (Wilson Bull. 88:509, 1976) reported Blue Jay predation on a mature Yellow-rumped Warbler (*Dendroica coronata*) in a residential section of Temple, Texas. Bent (U.S. Natl. Mus. Bull. 191, 1946) states that in addition to robbing nests of both eggs and young, the Blue Jay undoubtedly kills adult birds on occasion.

On 21 August 1977, I observed an attack by a Blue Jay on an adult, female House Sparrow (*Passer domesticus*) at Muhlenberg College in a residential area of Allentown, Pennsylvania. The sparrow was dust bathing in a parking lot while being watched by the jay perched less than 25 m away in a spruce tree. The jay dived and pounced on the sparrow and immediately began peeking it violently about the neck. A few seconds later the jay flew back to its perch leaving the stunned sparrow lying in the parking lot. Again the jay dived and pounced on the sparrow's back decapitating the bird with a few more pecks on the neck. The jay grabbed the sparrow's body in its claws and flew to the spruce where it began to feed. In a short while the sparrow's body was dropped to the ground and the jay flew out of sight. Inspection of the sparrow's body revealed that the jay had fed on the breast region after having plucked the feathers from the area.

Prior to the attack, both birds appeared normal and healthy. Observation of the sparrow revealed no conspicuous physical defects (such as difficulty in walking or flying) that might have attracted the Blue Jay's attention. Climatic and food stresses were probably not factors to be considered at this time of year. Perhaps dust bathing and its attendant postures and movements could have given an air of vulnerability to the sparrow.—TERRY L. MASTER, *Dept. of Biology, East Stroudsburg State College, East Stroudsburg, Pennsylvania 18301.* *Accepted 16 Nov. 1978.*

Wilson Bull., 91(3), 1979, pp. 470–471

Long-winged Harrier predation on Wattled Jacana eggs.—Long-winged Harriers (*Circus buffoni*) prey on small birds, mammals, and reptiles (ffrench, A Guide to the Birds of Trinidad and Tobago, 1973:113). Although they take eggs of various species of birds (Haverschmidt, The Birds of Surinam 1968:67), no records are available on the efficiencies and rates of egg predation. This note documents harrier predation on 3 nests of color-marked Wattled Jacanas (*Jacana jacana*) in coastal Guyana. The region consists of extensive rice fields crossed by dikes and canals. Observations were made with a 20× spotting scope from a 3 m-high house porch.

At 17:10 on 30 July 1977, we saw a single Long-winged Harrier cruising upwind 1–3 m above the vegetation. It hovered briefly, landed on the platform of a jacana nest that contained 4 eggs, and held its wings aloft as the pair of jacanas charged it giving alarm calls. An unmarked male jacana joined the pair in defending the nest. When not attacking the harrier, the jacanas remained 4–6 m away from it. The harrier made 4 trips to the nest, departing each time with an egg in its bill. Eggs were eaten about 30 m from the nest. The harrier revisited the empty nest twice within 5 min before departing from view. The platform of the nest was scrambled and no eggshells were found in the area.

On 11 August 1977, about 17:00, a Long-winged Harrier hovered briefly above a second nest that contained 4 eggs, and dropped out of sight for several min before rising, hovering, and descending at the same place again. After the fourth descent the harrier took flight and quartered another field. When we reached the nest all eggs were missing, the platform was disarranged, and the male stood nearby giving alarm calls. We found remains of 4 eggshells, at separate locations on the dike, about 15 m from the nest.

On 22 August 1977, about 17:30, we saw a harrier over another nest in the same drainage ditch as the second nest. The male had incubated 4 eggs since 10 August. Again the harrier made 4 descents, hovering briefly each time before dropping. Upon checking the nest we found both adults vocalizing nearby, the 4 eggs missing, and pieces of eggshells on the dike.

The 3 cases of predation were on nests that had contained 4 eggs earlier in the day. Because we were about 0.4 km away and these last 2 nests were obscured by vegetation, we couldn't see whether the harrier carried the eggs away. Here, evidence of predation is inferred primarily by harrier behavior. The jacana's anti-predator behavior was apparently ineffective against the harriers. The harriers revisited the nests within a short period of time until all eggs were removed.

The observations are interesting relative to the high rates of predation and nest destruction reported for Wattled Jacanas (Osborne and Bourne, Condor 79:98–105). Of 51 nests followed through hatching in the present study, 43 (84.3%) failed to produce at least 1 young. Twenty of 43 (51%) nest failures are attributed to egg removal by predators, 3 of these (13.6%) to Long-winged Harriers. It appears Long-winged Harriers are efficient and important predators on jacana eggs.

Research in Guyana was funded by grants to Osborne from the Alumni Foundation of Miami University.—David R. Osborne, *Dept. of Zoology, Miami University, Oxford, Ohio 45056* and Steven R. Beissinger, *1 Johns Road, Cheltenham, Pennsylvania 19012.* *Accepted 3 Oct. 1978.*

Wilson Bull., 91(3), 1979, pp. 471–472

Arboreal foraging by Cattle Egrets.—The Cattle Egret (*Bubulcus ibis*) is among the most versatile herons in foraging. It is known to use at least 14 foraging behaviors and forage in commensal association with a number of animals and other slow moving objects (Kushlan, *in* Wading Birds, Natl. Audubon Soc., New York, 1978:249–297). Typical foraging methods involve chasing prey or walking slowly on the ground stalking prey.

Neither Cattle Egrets nor other herons have been reported to forage arboreally, except to use branches as perches while fishing. I have seen 2 instances of Cattle Egrets foraging arboreally in south Florida. On 25 December 1976, I observed a flock of about 20 birds feeding while walking on pole bean (*Phaseolus vulgaris*) vines. This cultivated crop is supported by a trellis of poles and horizontal wires to a height of nearly 2 m. The Cattle Egrets walked on top of the plants while stabbing at potential prey. On 18 June 1978, an egret foraged on top of a closely trimmed, flat topped ixora (*Ixora coccinea*) hedge in Coral Gables, Florida. The egret walked slowly around the hedge, periodically stopping and stabbing or hopping and then stabbing.

Arboreal foraging is another of many examples of the versatility and adaptability of the Cattle Egret. This species is known to forage off the ground by riding on the backs of commensals from which it stabs at prey or hops to the ground when prey is seen (Skead, Ostrich Suppl. 6:109–139, 1966; Kushlan, op. cit.). Similar use of plants with a suitable structure is not a very different procedure so it is probably easily developed. The potential is not geographically restricted, as Lancaster (pers. comm.) has seen similar behavior by Cattle Egrets in Colombia. Probably the structure of natural vegetation rarely permits an agret to walk slowly on it, but plants cultivated for agricultural or horticultural purposes appear to provide suitable horizontal substrates for such an adaptable bird.

I thank Thomas C. Custer and Douglas D. Lancaster for comments on this paper.—JAMES A. KUSHLAN, *U.S. National Park Service, South Florida Research Center, Everglades National Park, Homestead, Florida 33030.* *Accepted 14 Nov. 1978.*

NEW LIFE MEMBER

Mr. Theodore W. Gutzke is now a life member of The Wilson Ornithological Society. Mr. Gutzke is wildlife biologist and assistant wildlife refuge manager of Great Swamp National Wildlife Refuge. His principal interests in ornithology are in waterfowl biology and ecology with an emphasis on habitat requirements and management applications. He has directed work on the Wood Duck and Canada Goose. Mr. Gutzke is a member of a number of natural history organizations. Bird watching, photography, camping, and gardening are activities Mr. Gutzke enjoys. He is married and has two children.

Wilson Bull., 91(3), 1979, pp. 473–476

ORNITHOLOGICAL LITERATURE

An Atlas of Speciation in African Non-Passerine Birds. By D. W. Snow (ed.). British Museum (Nat. Hist.), London, 1978: 390 pp., 391 maps. £42.50.—This important book is the joint effort of 14 compilers including the editor, who attempted to achieve uniformity of treatment by the contributing authors. It completes the great work started by Hall and Moreau on the passerine birds of Africa (1970). Together the 2 volumes provide a useful and reliable synthesis of data on the distribution, ecological occurrence, and evolutionary relationships of the breeding birds of Africa south of the Sahara. As in the earlier volume, no accounts or maps are given for species that are merely transient or wintering visitors in that vast region. Also excluded are such purely or predominantly marine groups as the penguins, gannets, tropicbirds, gulls, terns, skimmers, and marine species of cormorants. Included are the islands in the Gulf of Guinea, but not the Cape Verde Islands. On the east coast, Madagascar and the Comoros are dealt with only for species considered conspecific with, or in the same species-groups as African forms. Socotra, Zanzibar, Pemba, and Nafia are included as they are hardly more than sea-girt pieces of the African zoological region.

The maps attempt to show all recorded localities for all species included. When one realizes that in many species there are dozens or even hundreds of such records, the enormous amount of information brought together, and the ease with which the results may be assimilated, must make all users of the book aware of how much they owe to the authors. The hours of tedious library research involved in producing these maps will save many times as much time for the readers, often less well equipped with books and experience than the self-sacrificing compilers. The literature is covered up to the close of 1976, although a few 1977 references that add significant records were included as the work went to press.

Following the maps for each family is a short summary statement pointing out extra-limital ranges of the included or related species, and calling attention to obvious gaps or weaknesses in the current information on the African taxa. In cases where there are more non-African than African species, these statements help to place the African data in a better perspective. Thus, for the Columbidae (p. 220) we are informed that the family has a cosmopolitan distribution in tropical, subtropical, and temperate regions; that of the 40 genera and 290 species currently recognized, 6 genera and 34 species occur in Africa, and that of these all but 2 are endemic to Africa or extend, at most, to adjacent parts of southwestern Arabia.

One great advantage of the maps is that they include many unpublished records, the specimen bases of which are in the collections of the many museums whose curators supplied these otherwise unreported data. For some areas for which specimens and literature are meager, the compilers included unpublished observations by resident ornithologists. This has involved sight records for conspicuous or easily identified species, particularly for large birds seldom collected today. We are assured that for families or genera in which field identification of very similar species is difficult and hence open to doubt and criticism, the inclusions on the maps are limited to actual museum specimens with data. In the appendix at the end of the volume there is a complete list of the books and papers used in preparing the maps. To a long-time student of African ornithology it comes as a surprise that Anton Reichenow's great 3-volume *Die Vogel Afrikas*, the first comprehensive account of birds of the continent, is omitted. Also missing are Hubert Lynes' work on the birds of northern and central Darfur, Reginald E. Moreau's *The Bird Faunas of Africa and its Islands*, and V. G. L. van Someren's extensive 1922 and 1932 papers on the birds of Kenya and Uganda. These omissions can only mean that the records therein reported have since been repeated in other or more recent works, or that, in the case of Reichenow's work, the sources from which he obtained his data are themselves included. Another surprising omission is Stark and Sclater's 4-volume work on the birds of South Africa. One can only hope that all the specimen or observational records in these books have been incorporated in the present atlas. It is highly probable that these sources have not been overlooked by the experienced and competent experts who compiled the present series of maps, but it would have been good to see them duly listed.

In his introduction the editor writes that the primary objective of this enormous compilation was to complete the mapping of a major continental avifauna, and thereby to enable zoogeographers, evolutionary biologists, and other students of special areas or species to examine and analyze the speciation patterns of African birds insofar as they can be expressed geographically. He then states that a ". . . less clearly defined hope is that the presentation of the distributional and evolutionary complexities of a rich and ancient avifauna may suggest to future workers new lines of approach to evolutionary problems which at present we cannot clearly see." It is to be expected that such may well transpire; at least it will not be the fault of the authors if this does not happen. They have presented, in readily usable and easily grasped and compared form, a truly vast amount of data and ideas, a source for innumerable studies to come. Their combined efforts have resulted in a work that summarizes and presents in a critical, reliable, and meaningful manner the work of hundreds of devoted ornithologists over many decades, actually over 2 centuries, in an area of which parts are now unfortunately less accessible to visiting scientists than they once were. Because of the difficulties, uncertainties, and even conflicts attendant upon the organization and functioning of some "emerging" nations still too busy with basic necessities to afford leisure or opportunities for the study of their rich and fascinating birdlife, we may rejoice that in this atlas we have a masterly compilation of what has been learned to date. This we cannot lose, and when additions can be made, their accretion will be easy to fit into the picture and to assimilate into our concepts.—HERBERT FRIEDMANN.

LIFE HISTORY OF THE EASTERN FIELD SPARROW IN CALHOUN COUNTY, MICHIGAN. By Lawrence H. Walkinshaw. 1978: 153 pp., 40 figs., xerox copy of typescript. $21.50 (hard cover), $16.50 (soft cover) for persons affiliated with an educational institution; $27.00 and $22.00, respectively, for others. Order from: University Microfilms International, Dissertation Copies, 300 N. Zeeb Rd., Ann Arbor, Michigan 48106. Order No. LD 00185. —R.J.R.

THE BIRDS OF EAST AFRICA. A collection of lithographs prepared from the originals drawn from nature by V. G. L. van Someren between the years 1909 and 1937. A Limited Edition. Published by A. C. Allyn, for the Allyn Museum of Entomology, Sarasota, Florida, Volume I, Ploceidae–1, Plates 1–93, (color) 1973. $60 per volume, $6 per fascicle of 16 plates.—Over 1800 different kinds of birds painted from life in their natural habitat by V. G. L. van Someren (1886–1976) are included in this collection, of which the weaverbirds comprise the first and, so far, only volume. The frontispiece is a fine color photograph of the author in old age. The series is intended for museums, libraries and collectors of fine illustrations in natural history. Arthur C. Allyn, the publisher, is himself a collector and a benefactor of much naturalist research.

There is a foreword by Dr. Austin L. Rand, formerly Chief Curator, Department of Zoology, Field Museum of Natural History, Chicago. Dr. Rand had previously written a brief summary of van Someren's life and contributions to ornithology in the Bulletin of the Field Museum (April, 1950), and also edited *Days with Birds*, a 520-page book (1956) by van Someren, which was 1 of the first general surveys of the behavior of East African birds. It was based on personal observations by the author, and still has some of the most extensive life histories yet available on these birds.

Dr. V. G. L. van Someren was a man of many talents and accomplishments. He graduated in medicine and dental surgery from the University of Edinburgh and was appointed medical officer in British East Africa (Kenya). In addition to his duties as a medical doctor, he studied the natural history of East Africa for over 40 years. In 1906 he and his brother started a systematic survey of the birds of Kenya and Uganda, and ultimately over 25,000 specimens from their collection were deposited in various museums. Part of his collection of nests and eggs of East African birds is now in the collection of the Western Foundation of Vertebrate Zoology in Los Angeles. Dr. van Someren also made over 5000 photographs, some of which help illustrate the volumes by Macworth-Praed and Grant on *Birds of Eastern and North Eastern Africa.* He was interested in all phases of natural history, was Honorary Curator of the Natural History Museum at Nairobi (1914–38), a Fellow of the Linnaean Society of London and a Fellow of the Royal Entomological Society. He was also Director of the Coryndon Memorial Museum, Nairobi (1938–40).

Another talent is now made generally evident with the publication of this collection of lithographs; V. G. L. van Someren could also do superb illustrations of birds in their natural habitat. The pictures of the birds are lifelike and scientifically accurate (including color of bill and eye) and show each bird, often both male and female, in its natural habitat, perched in characteristic vegetation. The depiction of the nests of the weaverbirds are only used in the general background, and show little detail; the bird itself takes pre-eminence in each illustration. With a few exceptions, the drawings of the nests are generally accurate. However, the nest of Large Solitary Golden Weaver (*Ploceus xanthops*) should not have an entrance tube, and that of Black-billed Sparrow Weaver (*Plocepasser mahali*) is not pensile from the roof as shown. Each plate is labelled on an interleaf with the scientific name in capital letters followed by an English name in small letters. A paragraph or 2 of descriptive material accompanies each plate and gives some brief notes on general habits as well as on the usual clutch size and the color of the eggs of each species.

The first volume on weaverbirds illustrates most of the species of East African Ploceidae, not including the sparrows. It includes the long-tailed viduine finches, but not the estrildid finches. This work must be viewed historically, and one must keep in mind that the illustrations were done many years ago. Some of the scientific names are outdated, for example, *Ploceus nigriceps* is used for *Ploceus cucullatus nigriceps* (Layard's Black-headed Weaver) and *Urobrachya axillaris* for *Coliuspasser axillaris* (Fan-tailed Widow-bird). The historical flavor is reflected in the English names that van Someren created for his birds, there being rather few such names in general use at that time. Not infrequently his names seem more appropriate than those now in general use. For example, "Grey-capped Social Weaver" more precisely describes *Pseudonigrita arnaudi* than does "Grey-headed Social Weaver," the name found in some recent books, since this species does have a gray crown while the rest of the head is definitely not gray. Similarly, van Someren's "Yellow-cheeked Black Weaver" is far more descriptive of the distinctive features of *Ploceus melanogaster* than is "Black-billed Weaver" of more recent works. Van Someren described a number of new subspecies of weaverbirds, and there is rather considerable and useful illustration of subspecies in the book; back in those days what was or was not a different species was not nearly so clear as it seems today.

It is a pity that the work of this great ornithological pioneer is marred by inadequate editing. Misspellings of the scientific names are not uncommon, and some are not corrected by the all too brief "Errata" sheet that accompanies the volume. Two plates are erroneously labelled. In Plate 8 the lower figure is obviously *Sporopipes frontalis*, the Speckle-fronted Weaver, and not *Pseudonigrita darnaudi* [sic] *dorsalis.* Plate 66, labelled *Euplectes hordacea*, really shows *Euplectes orix.* There is no table of contents and no index, and to find a given species one must simply page through the book.

Despite its venerable nature this collection reminds us we still have much to learn about East African birds. For example, as yet there is very little known about *Ploceus* (*Anaplectes*) *jubaensis*, a rather spectacular bird (apparently a subspecies of *rubriceps*) which van Someren described in 1920 and which he calls the Juba River Scarlet Weaver. He also notes an observation of nest building for Weyn's Weaver (*Ploceus weynsi*), a Ugandan species of which the nest and eggs seem to be still undescribed.—NICHOLAS E. COLLIAS AND ELSIE C. COLLIAS.

NEW LIFE MEMBER

Dr. Jerrold H. Zar, a recent Life Member of The Wilson Ornithological Society, is Professor and Chairman of Biological Sciences at Northern Illinois College in DeKalb. Dr. Zar's principal interests are physiological adaptations to environmental stress and statistical analysis of orientation and other data. He has had two books published—one entitled Biostatistical Analysis and the other Field and Laboratory Methods for General Ecology. Dr. Zar is active in many professional societies and is married with two children.

Wilson Bull., 91(3), 1979, pp. 477–478

PRESIDENT'S MESSAGE

This issue of the *Bulletin* is much smaller than the past several issues, and indeed is much smaller than we would like it to be. The reason is simple. For sometime now the Society has been living beyond its income in so far as the *Bulletin* is concerned, and now the day of reckoning is at hand. We must retrench by publishing smaller issues until our financial position improves. The alternative is another healthy increase in dues, which we hope to avoid, at least for a while.

The financial position of the Society would be greatly improved if the membership were larger. The interest in birds among the general public has grown tremendously in the last decade, increase in membership in the Wilson Society has not increased proportionally. The Society has always stressed its interest in the serious amateur student of birds and surely there are still many who would enjoy and profit from a membership in the Society. Almost every member must know at least one such serious birder who would be a candidate for membership. If you desire to nominate persons for membership send the names and addresses to the Chairman of the Membership Committee, **Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, WV 26506.** A modest goal for 1980 would be a one-third increase in membership.

George A. Hall, *President*

ORNITHOLOGICAL NEWS

THIRD JOINT COS-WOS MEETING IN 1980

The third joint meeting of The Cooper Ornithological Society and The Wilson Ornithological Society will be held in Corpus Christi, Texas, at the La Quinta Motor Inn from 19–23 March 1980. Paper sessions are scheduled to start the morning of 20 March. The announcement of schedule and arrangements, and a call for papers, will be mailed to members of COS, WOS and AOU using the new Ornithological Societies of America mailing labels. This mailing is scheduled for 1 December 1979. The sponsoring organizations of the meeting are Corpus Christi State University and the Coastal Bend Chapter of the National Audubon Society. Chairpersons of the committees on arrangements and on scientific program are, respectively, Brian R. Chapman, Division of Biology, Corpus Christi State University, Corpus Christi, Texas 78412, and Jerome A. Jackson, Department of Zoology, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

XVIII INTERNATIONAL ORNITHOLOGICAL CONGRESS—1982

The XVIII International Ornithological Congress will take place in Moscow, USSR on 16–25 August 1982. Professor Lars von Haartman (Finland) is President and Professor Valery Ilyichev (USSR) is Secretary-General. The program is being planned by an international Scientific Program Committee chaired by Professor J. Aschoff (Germany). Current plans are to have a plenary lecture each morning followed by symposia; hopefully, only three symposia will run concurrently at any time. One mid-congress day will be free. Postcongress excursions are planned to many interesting ornithological localities, such as

Baikal, Samarkand and Bochara. If sufficient interest exists, a group flight will be arranged for North American ornithologists.

Inquires about the congress and requests for application forms should be addressed to:

Professor Valery Ilyichev
Secretary-General
XVIII Congressus Internationalis Ornithologicus
Ringing Centre 117312
Moscow, Fersman Street 13
USSR

Questions and suggestions (including for the program and flight plans) may be sent to:

Dr. Walter Bock
Department of Biological Sciences
Columbia University
New York, New York 10027

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student membership awards in The Wilson Ornithological Society are available because of funds generously donated in the memory of Aaron M. Bagg, a former president of the Society. Application forms for the awards to be granted in 1980 may be obtained from John L. Zimmerman, Division of Biology, Kansas State University, Manhattan, Kansas 66506. The deadline for applying is 1 November 1979. A Bagg Student Membership Award provides a 1 year membership in the Wilson Society for successful nominees.

PAUL A. STEWART AWARDS

The Paul A. Stewart Fund for Ornithological Research has been established by donations from Paul A. Stewart. Income from this endowment will be awarded annually to support research in ornithology, especially studies of bird movements based on banding and analyses of recoveries and returns and investigations pertaining to economic ornithology. Several Stewart Awards in the amount of $200.00 each will be available each year. Stewart Awards will be equally available to students, amateurs and professionals. Interested persons may write to Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. Completed applications must be received by 1 Feb. 1980. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 19–23 March 1980.

NEED TO COMPLETE YOUR SET OF *THE WILSON BULLETIN*?

Selected out-of-stock back issues are now being reproduced. These are exact duplicates of the originals; color plates are reproduced in black and white. All volumes from 1889, volume 1, to date will be available. Reproduction schedules will depend on the interest shown, so please respond promptly. Prices will be the same as current rates. Special prices will be quoted for quantity orders. Please send enquiries to Dr. Robert D. Burns, Treasurer, Dept. of Biology, Kenyon College, Gambier, Ohio 43022 U.S.A.

Wilson Bull., 91(3), 1979, pp. 479–494

PROCEEDINGS OF THE SIXTIETH ANNUAL MEETING

Curtis S. Adkisson, Secretary

At the invitation of the Nebraska Ornithologists' Union and the University of Nebraska at Omaha, the sixtieth Annual Meeting of the Wilson Ornithological Society was held at the Howard Johnson Convention Center in Omaha, Nebraska, from Thursday, 5 April to Sunday, 8 April 1979. The Executive Council met on Thursday evening and Saturday afternoon. Business and scientific papers' sessions were held in the International Room on Friday and Saturday. An informal open house, hosted by the Nebraska Ornithologists' Union, was held in the International Room Thursday evening. A program of slides was presented by Dr. Paul A. Johnsgard at the open house. Later that evening, a film, "Wild Chorus" by Mr. Glen Chambers, was shown in the International Room.

The Annual Banquet was held Saturday evening, and Mr. Chambers presented a slide show on American wildlife, and offered tips, based on his long experience in the field of wildlife photography, on how one can improve one's own photographic efforts.

There were field trips on Friday to see waterfowl concentrations along the Missouri River floodplain, on Saturday to see birds, primarily passerines, in the Fontenelle Forest, and on Sunday to see concentrations of migrating Sandhill Cranes and to visit a Prairie Chicken lek site.

FIRST BUSINESS MEETING

The session was called to order at 9:15, Friday, 6 April by Local Committee Chairman. Roger Sharpe, who introduced Nebraska Ornithologists' Union Vice-President Ruth Green. Mrs. Green spoke briefly in welcoming the Society to Nebraska. President James responded to her welcome, commenting that the Society had met in Omaha in 1946, the first meeting of the Society in 5 years. At that meeting George Sutton became president of the Society, and N. Tinbergen gave a paper on bird behavior. President James then called to order the first business meeting. He announced that due to the airline strike the Treasurer could not attend the meeting, and his report had not yet arrived. For the same reason, there was no list of new members for posting. He appointed Robert Burns chairman of the Resolutions Committee.

Secretary C. S. Adkisson summarized the actions taken by Executive Council on Thursday evening:

1. The council heard all officers' and committee reports except that of the Treasurer. This report will be presented at the second business meeting.
2. Editor Jon C. Barlow was unanimously re-elected.
3. Council approved the recommendations of the committees on awards. Winners of awards will be announced at the annual banquet.
4. The Society will meet next year from 19 to 23 March 1980 in Corpus Christi, Texas, at the La Quinta Royal Motel, jointly with the Cooper Ornithological Society. Brian Chapman of Corpus Christi State University is chairman of the Local Committee.

   The Council has accepted the invitation of the Canadian Wildlife Service to meet in 1981, in Sackville, New Brunswick, from 4 to 7 June. A firm date has been established for the 1982 meeting, to be held on the campus of Virginia Polytechnic Institute and State University, Blacksburg, Virginia, from 6 to 9 May.

Following the Secretary's report, President James introduced Peter Hicklin, of the Canadian Wildlife Service, who summarized accommodations and field opportunities for the 1981 meeting in Sackville, N.B.

President James introduced Bulletin Editor, Jon C. Barlow, who presented a summary of his report to the membership.

Following announcements by Local Chairman Sharpe and Program Chairman Gaunt, the meeting was adjourned.

REPORT OF THE EDITOR—1978

Though the job is a time-consuming one, I enjoy editing *The Wilson Bulletin.* Until now, I have made few changes in emphasis, feeling that Dr. Jackson did an excellent job as editor. Basically I am following procedures developed by Jerry Jackson and earlier editors. In order to keep Xeroxing costs to a minimum, I have indicated to authors that 3 copies of their manuscript rather than two should be sent to the Editor; only that major change has been made.

From the time that I began as editor in May 1978, I have received just over 300 manuscripts either rerouted through Dr. Jackson, or from new authors. Of these, 137 manuscripts were new, the others at some stage of the editorial process. Status of manuscripts at present in some stage of the editorial process is:

Status[1]	Numbers		
	Notes	Papers	Total
Published	20	10	30
Acknowledged			12
Referees requested			6
At 2 referees			4
At 1 referee			22
Referee reports received			25
Manuscripts returned for revision			51
Revisions received			30
Accepted			70
Rejected			27

On an issue-by-issue basis, the following is the status of volumes 91 and 92:

Volume 91

No. 1, March: 176 pp., 10 papers, 20 notes, 13 reviews, 1 page of news, Proceedings of the Fifty-ninth Annual Meeting. Published 27 April 1979.

No. 2, June: ca. 180 pp., 11 papers, 14 notes, 6 reviews, 1 page of news, 1 page suggestions to authors.

No. 3, September: pp. unknown, 11 papers, 11 notes, Proceedings of the Sixtieth Annual Meeting.

No. 4, December: pp. unknown, 8 papers, 16 notes.

Volume 92

No. 1, March: pp. unknown, 3 papers, 9 notes.

No. 2, June: pp. unknown, 6 papers, 6 notes.

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[1] All figures updated to 1 June 1979.

This has been a year of transition with Dr. Jackson receiving perhaps more new manuscripts than I as our authors adjusted to the change in editorship. In the first half year, a deluge of manuscripts arrived in my office, directly, or rerouted through Dr. Jackson. Though this large number of manuscripts initially slowed down the editorial process, we are now beginning to reduce the backlog. A strong response from referees was most helpful in keeping abreast at the onset, however more recently, it has been difficult to locate two evaluators with speed.

We will not have published the last of the manuscripts originally submitted to Dr. Jackson until sometime in 1980. Thus, it is difficult to be certain what our turn-around time is going to be. At present, it appears to be in the order of 16 months for both notes and major papers, from time of first receiving a manuscript. From date of acceptance to publication the lag is about 1 year.

I have appreciated the patience and assistance of both authors and referees in this initial period of adjustment and hope that *The Wilson Bulletin* continues to meet with the satisfaction of members.

Jon C. Barlow, *Editor*

THE WILSON ORNITHOLOGICAL SOCIETY

REPORT OF THE TREASURER

Year Ending 31 December 1978

GENERAL FUNDS

Balance as of last report, 31 December 1977			$18,463.65

RECEIPTS

Membership Dues			
Active for 1978	$ 5,202.00		
Active for 1979	10,162.00		
Total Active		$15,364.00	
Sustaining for 1978	765.00		
Sustaining for 1979	780.00		
Total Sustaining		1,545.00	
Subscriptions to *The Wilson Bulletin*			
For 1978	2,330.00		
For 1979	3,960.00		
Total Subscriptions		6,290.00	
Advance Renewals		320.00	
Sales of Back Issues of *The Wilson Bulletin*		2,461.50	
Interest and Dividends on Savings & Investments			
Income from General Endowment Fund	5,416.39		
Income from G. M. Sutton Colorplate Fund	1,970.78		
Income from Paul A. Stewart Fund	1,199.78		
Interest on Endowment Savings Account	730.88		
Total Interest and Dividends		9,317.83	
Royalties from Microfilming Back Issues of *The Wilson Bulletin*		252.35	

Contributions from Authors and Others	1,543.00	
Annual Meeting Excess	1,026.89	
Total Receipts		$38,120.57

DISBURSEMENTS

The Wilson Bulletin (Printing & Engraving)	$36,361.10	
The Wilson Bulletin (Mailing & Maintenance)	6,142.68	
Colorplate Processing Expense	3,041.00	
Editor's Expense	1,990.21	
Secretary's Expense	91.42	
Treasurer's Expense	2,049.49	
Committee Expense	115.04	
President's Expense	29.74	
International Council for Bird Protection	30.00	
Annual Meeting Expense	674.00	
Miscellaneous Expense	38.00	
Total Disbursements		$50,562.68

GENERAL CASH FUNDS

Checking Account Balance in Old Kent Bank & Trust Company, Grand Rapids, Michigan, 31 December 1978	$ 6,021.54

JOSSELYN VAN TYNE MEMORIAL LIBRARY FUND

Balance as of last report, 31 December 1977	$ 530.58

RECEIPTS

Sale of Duplicates and Gifts	$ 1,073.11

DISBURSEMENTS

Purchase of Books	$ 1,041.37
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1978	$ 562.32

LOUIS AGASSIZ FUERTES RESEARCH FUND
MARGARET MORSE NICE FUND
EDWARDS AND W.O.S. PAPER FUNDS

Balance as of last report, 31 December 1977	$ 1,746.50

RECEIPTS

Contributions	$ 622.00

DISBURSEMENTS

Grant-In-Aid	
To David Raimist	$100.00
To Alexis Maclean	200.00

To Richard Brewer and Lynda Swander	225.00	
To Wayne Weber and John Theberge	125.00	
To Susan Hilsenbeck	100.00	
Total		$ 750.00
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1978		$ 1,618.50

Aaron Bagg
Student Membership Award Fund

Balance as of last report, 31 December 1977	$ 154.00
RECEIPTS	
Contributions	$ 200.00
DISBURSEMENTS	
Student Membership Grants	$ 180.00
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1978	$ 174.00

Endowment Funds
General Endowment Fund

Balance in Endowment Savings Account, Old Kent Bank and Trust Company, Grand Rapids, Michigan, as of last report, 31 December 1977		$ 22,400.00
RECEIPTS		
Life Membership Payments and Contributions		$ 3,323.50
Stewart Fund		10,000.00
		$ 13,323.50
DISBURSEMENTS		$ 25,270.15
Balance in Endowment Savings Account, Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1978		10,453.35
Investments Held as of 31 December 1978		
United States Government Bonds	$ 4,770.30	
Government Guaranteed Bonds	9,800.00	
International Bank Bonds	8,808.75	
Canadian Provincial Bonds	3,756.25	
Corporate Bonds	27,980.00	
Convertible Corporate Bonds	1,850.00	
Convertible Preferred Stocks	7,432.50	
Common Stocks	50,146.75	
Uninvested Principal	253.76	
Total Investments		$114,798.31
Total General Endowment Fund, 31 December 1978		$125,251.66

GEORGE MIKSCH SUTTON COLORPLATE FUND

Investments Held as of 31 December 1978		
International Bank Bonds	$ 978.75	
Canadian Provincial Bonds	4,356.25	
Corporate Bonds	9,112.50	
Common Stocks	11,225.00	
Total Investments		$ 25,672.50

PAUL A. STEWART FUND

RECEIPTS	$ 20,000.00
DISBURSEMENTS to Investing Trustees	20,000.00
Total Combined Wilson Ornithological Society Endowment Funds, 31 December 1978	$150,924.16

Ernest E. Hoover, *Treasurer*

REPORT OF THE INVESTING TRUSTEES—1978

Again this year the Trustees invested grudgingly and cautiously in view of continuously rising interest rates, preferring to keep some funds available for investment when a more optimistic climate seems nearer.

With income in mind, we made 3 new purchases in 1978:

(1) for the Sutton Colorplate Fund, 200 shares of Duke Power Co. common stock on 14 March at 20 to yield 8.6%,

(2) for the General Endowment Fund, $10,000 U.S. Government Guaranteed 9¼% ship bonds due 2003 at 104½ to yield 8.8% on 9 May, and

(3) $10,000 Citicorp floating rate notes, 9% due 1998 to yield just over 9% on 15 November. These AAA bonds bear an interest rate coupon which changes each 6 months dependent upon U.S. Treasury Bill rates at the time, and the rate for the 6 months beginning 1 March will be in the neighborhood of 11 to 11.10%. Such a delightful return, we must caution, is only assured for 6 months and then could be higher or lower, but we will appreciate this increment to our income while it lasts.

There have been several dividend increases since our last report, some small help in trying to keep our income abreast of the inflation rate, a rate which shows little sign of moderating in the near future.

We also received a 100% stock dividend from Owens Corning Fiberglas, increasing our holding to 100 shares.

Expected income from investments in 1979, excluding savings bank interest, should be in the neighborhood of $8100 in the General Fund (including the Stewart Fund) and $2175 in the Sutton Colorplate Fund. If we should invest some of the savings account funds later this year, which we will probably do if interest rates climb still more, the estimate for the General Fund would increase somewhat.

Phillips B. Street, *Chairman*

AUDITOR'S REPORT

To: The Wilson Ornithological Society.

We, the undersigned, have examined the Treasurer's records, bank statements, cancelled checks, account books and other financial records of the Society covering transactions occurring during the past fiscal year. The financial status of the Society is substantially as set forth in the Treasurer's report dated 31 December 1978.

Our examination has ascertained that all income has applied to the proper funds and no expenditures have been made except as authorized.

James F. Ponshair, *Member*
George M. Wickstrom, *Member*

REPORT OF THE NOMINATING COMMITTEE—1979

All of the following individuals have been contacted by letter and each has returned a favorable response indicating that they would serve if elected or continue to serve the Society in their current office:

President—George A. Hall
First Vice-President—Abbot S. Gaunt
Second Vice-President—Jerome A. Jackson
Secretary—Curtis S. Adkisson
Treasurer—Ernest E. Hoover
Editor—Jon C. Barlow
Executive Council Member—Richard C. Banks

Sidney A. Gauthreaux, Jr., *Chairman*
Kenneth C. Parkes
Andrew J. Berger

REPORT OF THE MEMBERSHIP COMMITTEE—1978

During the past year a great deal of work has gone forth on compiling the joint membership list of the A.O.U., C.O.S. and W.O.S. Three W.O.S. members, Toby and Sandy Gaunt and Bob Whitmore, have worked on the joint membership list committee. The anticipated list should be functional for next year's mailing.

In response to advertisements placed in *The Auk*, *The Condor* and *The Wilson Bulletin*, 88 requests for membership have been received by the membership chairman, many containing dues payments. I feel advertisements of this nature should be done once each year.

Robert C. Whitmore, *Chairman*

REPORT OF THE STUDENT MEMBERSHIP COMMITTEE—1978

Letters requesting membership nominations of students interested in ornithology and inviting application from exceptional students to be considered for Aaron M. Bagg Student Membership Awards were sent to more than 200 college and university faculties throughout North America. This activity resulted in 22 applications for the Bagg Award; 18 were selected as award recipients. Award recipients will be announced in a forthcoming issue of *The Wilson Bulletin*. About 25 individuals were nominated for membership in the

Society. These nominees received a letter from the Student Membership Committee and also a letter from a group of graduate student members. The latter was designed to present the advantages of membership from the perspective of active student members.

James R. Karr, *Chairman*
Roland R. Roth
Stephen M. Russell
Elliot J. Tramer

REPORT OF THE LIBRARY COMMITTEE—1978

Calendar 1978 saw generally normal operations for the Josselyn Van Tyne Memorial Library, with steady progress and expansion, under the direct supervision of Janet Hinshaw with occasional consultations and collaborations by the rest of our Committee.

Checking, cataloging, and reshelving have taken a great deal of time; as a result, records are constantly being corrected and brought up to date. With the able assistance of Linda Lutz, an inventory of books is being completed and duplicate periodicals are being sorted out for future disposal. Long-standing discrepancies in such matters as exchange lists are given attention as time permits. Storage, not only of our circulation collection of books, periodicals, and separates, but also of duplicates and of "Bulletin" back issues, presents never-ending problems. However, progress, as usual, is being made on keeping things available and in proper order.

In the December 1978 issue of *The Wilson Bulletin* appears a list of the periodicals currently received. Reprints of the list are available; members are urged to refer to it, and to avail themselves of material they need—while, incidentally, noting any gaps in our series they might be able to help fill.

Through 113 "Bulletin" exchanges, we received 144 current journals, newsletters, and reprints. With 40 gifts and complimentary subscriptions, we received a total of 184 items.

Sale of duplicates augmented our New Book Fund by $243.25. Purchases from this fund brought us 36 new books, journals, and records.

We have 36 donors to thank for 1787 items presented to the Library: 55 books, 598 periodical issues, 20 reports and pamphlets, 1106 reprints, 4 translations, and 1 thesis. The donors were: K. A. Arnold, L. M. Bartlett, A. J. Berger, C. E. Bock, H. Brackbill. P. Brodkorb, G. A. Clark, R. Clement, C. Collins, R. A. Dolbeer, T. Dunstan, J. Gray (Forbush Bird Club), K. W. Haller, J. Jackson, J. Jehl, J. C. Jones, D. W. Johnston. L. Kelso, R. S. Kennedy, R. Kimmel, L & P Press, H. Mayfield, T. R. Miley, H. C. Mueller, J. C. Ogden, S. L. Olson, R. B. Payne, T. D. G. Rich, P. Schlatter (Toledo Naturalists' Association), A. Simon, W. E. Southern, P. Stettenheim, J. G. Strauch, Jr., A. Thoresen, G. Watson (A.O.U. Committee on Foreign Translations), J. D. Webster, L. R. Wolfe, and G. Woolfenden.

As for several years, special note must be taken of the contributions of past president, Andrew J. Berger, whose 784 items (including 623 reprints) made up nearly half of the total received.

During the year, 78 loans were made; these comprised 320 books, journals, reprints, photocopies, and translations.

As always, we express thanks for help, urge members to further cooperate, and invite further use of our growing facilities. We hope our services have been helpful.

William A. Lunk, *Chairman*

REPORT ON THE ICBP–US SECTION MEETINGS—1978

During 1978, the ICBP–US national section approved and began to implement the recommendations of its special committee concerning the future role and priorities of the organization. Generally, these are as follows:

1. The U.S. section will act as a forum for the exchange of information and ideas between the ornithologists and organizations which make up its membership.
2. It will act to identify conservation issues affecting birds in a timely and professional way.
3. It will act to provide liaison between non-governmental and governmental wildlife organizations, with regard to avian conservation.
4. It will act to help insure the quality of environmental programs by issuing policy statements and commenting upon such programs.

In carrying these roles out, ICBP–US is not suited to raise, nor can it readily be organized to raise significant new monies for field research and conservation projects. It is suited to fulfill an overseeing role because of its unusual aggregation of professional ornithologists from scientific and conservation organizations. It is not adequately relating to ICBP–International in its inherent responsibility to identify projects and problems requiring attention or to other conservation organizations needing expertise in ornithological conservation or to scientific organizations that could direct research to such problems. It has not adequately narrowed the geographic limitations of its interest to fulfill its proper place in the ICBP Constellation.

In line with these recommendations, the ICBP–US section is now meeting twice yearly, and is actively concerning itself with conservation issues in the areas outlined above. It has been decided that the section should actively involve itself only with bird conservation problems concerning the U.S., Central and South America; the latter two are included as areas of our concern as U.S. birds winter there. The only exceptions will be when U.S. government or private organizations are directly involved in conservation issues elsewhere in the world. In that case, we might involve ourselves as well.

For instance, in dealing with recommendations from the ICBP World Conference for its national sections, we considered only ones we felt applied to us. Among these were: pesticides in the tropics. AID is no longer recommending the use of pesticides because of U.S. laws but the World Bank is. A world convention is suggested to publicize the problems of pesticides; ICBP–US can get involved through dealing with U.S. companies still selling pesticides.

Darien Gap Highway through Panama.—ICBP–US will contact the Dept. of Agriculture which is already concerned over the possibility of the spread of animal diseases from south of Panama into the U.S.

Restricting wild bird trade.—Our concern will be to get the U.S. to again publish a total list of imports from all 80-odd ports of entry. Presently, each port keeps its own list and it is not published.

ICBP–Int. also has a bird conservation program of specific considerations under several broad criteria. It will be continually worked on and updated. ICBP–US is planning a similar program of specific considerations which also will be continually changing according to need.

Financially, ICBP–Int. has restructured its dues schedule according to the affluence of member countries. The U.S. section will be paying $1600 annually. In turn, we have had to raise our dues to help cover this rise. Organizational members will pay $100; we are also trying to expand our categories of non-voting members.

Concerning the special fund covering Ridgely's *Birds of Panama*, there is now enough in it to publish a Spanish edition if a translator can be found.

In order to become more visible as a conservation organization, to give members (especially non-voting ones) a concrete return for their dues and, most importantly, to make a significant contribution to bird conservation literature, the U.S. section is planning to publish a Yearbook of bird conservation. It would summarize bird conservation problems and activities taking place during the preceding year within the U.S. or as a result of U.S. activities abroad.

Dr. Stan Temple of the University of Wisconsin has tentatively made arrangements with the Univ. of Wisconsin Press to publish the yearbook as a 6 by 9 in paperback of 204 pages with black and white photographs, tables and an index. The printing would be done on a "belt press" so that even small additional runs could be made with little extra cost. Thus additional demands in the future can be met with relative ease. The initial printing would be 10,000 copies each selling for $4.95. The Univ. of Wisconsin Press will finance the publishing of the initial volume and ICBP–US would just have to meet advertising and distributing costs. We would want to advertise it through member organizations such as The Wilson Society. The Univ. of Wisconsin Press would also advertise it through its mailing lists, mostly to libraries, universities and other large institutions and would expect to sell many copies this way. The Yearbook should become an important reference and contribution to ornithological and conservation literature.

H. Lapham, *W.O.S. Representative*

SECOND BUSINESS MEETING

President James called the Second Business Meeting to order at 15:00 on 7 April 1979. Past President P. B. Street summarized the report of the Treasurer, and read the report of the Auditing Committee, both of which were accepted. The Secretary read the list of deceased members that have been brought to Council's attention.

S. A. Gauthreaux read the report of the Nominating Committee, which proposed the following slate of officers: President, George A. Hall; First Vice-President, A. S. Gaunt; Second Vice-President, J. A. Jackson; Secretary, C. S. Adkisson; Treasurer, E. E. Hoover; Elected Council Member, term to expire 1982, R. C. Banks. There being no further nominations from the floor, nominations were closed. The membership directed the secretary to cast a unanimous ballot for the proposed slate.

The following resolutions were read and passed at the second business meeting:

WHEREAS, the Wilson Ornithological Society has held its 60th annual meeting in Omaha, Nebraska, 5 through 8 April 1979, and

WHEREAS, the members have benefited greatly from the efforts of the local committee, chaired by Roger Sharpe, and the facilities of the Howard Johnson Convention Center, therefore

BE IT RESOLVED that the Wilson Ornithological Society extends its sincere appreciation to the Nebraska Ornithologists' Union and the University of Nebraska–Omaha, and to the local committee on arrangements for their contributions toward providing this memorable meeting.

WHEREAS, The Wilson Ornithological Society has returned to Omaha, Nebraska, to hold the 60th Annual Meeting of the Society on 5 to 8 April 1979, and

WHEREAS, both the paper sessions and the symposium on Birds with Restricted Ranges were of great value and inspiration, and

WHEREAS, we wish to recognize the work of the Local Committee on Arrangements for handling the ever increasing details related to overseeing the annual meetings,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society gratefully thanks the Scientific Program Committee, and the Local Committee on Arrangements, especially its chairman, Roger Sharpe, and also Lynne Vacanti for her special extra help which made for a most memorable and enjoyable meeting.

WHEREAS, The Wilson Ornithological Society recognizes those natural resources collectively identified as "nongame" as a major component of our Nation's fauna, and

WHEREAS, the need for detailed research and affirmative management of nongame resources is of paramount concern, and

WHEREAS, pending federal legislation proposing an excise tax on certain outdoor equipment, bird seed, and related materials may incur revenues of $20 to $30 million annually expressly for research and management of nongame animals,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society heartily endorses and supports passage of legislation which will provide funds expressly for research and management of nongame animals.

At the awards ceremony Saturday evening the following awards and prizes were announced:

Margaret Morse Nice Award

Craig T. Perdue, "Habitat component and statistical favorability correlates of American Robin reproductive success"

Louis Agassiz Fuertes Grant

Patricia A. Gowaty, "The evolution of monogamy in Eastern Bluebirds"

Edwards Prize

Glen E. Woolfenden, "Growth and survival of young Florida Scrub Jays" (Wilson Bull. 90:1–18)

Edwards Prize, Second Award

David G. Ainley, Robert C. Wood, and William J. L. Sladen, "Bird life at Cape Crozier, Ross Island" (Wilson Bull. 90:492–510)

Paul A. Stewart Awards

Robert R. Cohen, "Demography and population dynamics of the Tree Swallow in the Rocky Mountains of North-central Colorado"

Christopher J. Herlugson, "Biology of sympatric populations of Western and Mountain bluebirds"

Susan Hannon, "An investigation of territorial behavior in female Willow Ptarmigan and its relation to population regulation"

Bruce H. Pugesek, "Reproductive effort in a long-lived species"

Alexander Wilson Prize

Peter Hicklin, "Feeding ecology of migrant shorebirds in the Bay of Fundy"

REPORT OF THE SECOND VICE-PRESIDENT—1978

For this year's meetings at Omaha, we received 57 abstracts, 25 were from students, for submitted papers. This represents a substantial increase over last year in both student participation and total number of papers.

The large number of submitted papers provides the Program Officer with both advantages and disadvantages. On the one hand, a large number of papers insures that many will deal with similar topics and can be clustered. In some cases it is possible to build mini-symposia. On the other hand, concurrent sessions are necessary.

In addition to the submitted papers, we presented a symposium on "The Biology of Birds with Restricted Ranges." The symposium was co-organized by Jon Barlow and me, and I am extremely grateful to Jon, who generated most of the ideas while I confined myself to paper shuffling.

If we continue to have the response we have had for the last 2 years, the future Program Officers may have to pursue the necessity of rejecting some submitted papers or adopting techniques (such as poster sessions) that will permit us to continue to present large numbers of submitted papers. We also need to consider whether a symposium is necessary at every meeting. The best symposia occur when someone, often other than the Program Officer, has an idea and is willing to do some creative organizing. The Program Officer, of course, can do most of the busy work. In the absence of symposia, we might announce that certain sessions will be designated for certain topics and request papers to be submitted on those topics.

This office has not in the past had a budget. On the basis of my experience this year, I am requesting $75 for phone and mailing costs for the Program Officer.

In conclusion, the programming problems that we have or can foresee, appear to be those of excessive good health. I am certainly much happier worrying about how to accommodate all the people who wish to talk than I would be trying to determine how to fill sessions.

Abbot S. Gaunt, *Second Vice-President*

PAPERS SESSION

P. A. Johnsgard, University of Nebraska–Lincoln, *Ornithogeography of the Great Plains.*

C. E. Braun, Colorado Division of Wildlife, *The American Coot in Colorado.*

C. Leck, Rutgers, The State University, *Recent additions to the breeding fauna of New Jersey.*

S. D. Fretwell and R. Birdsell, Kansas State University, *Population declines in the Dickcissel.*

R. C. Banks, National Fish and Wildlife Laboratory, Washington, D.C., *The size of early Whooping Crane populations.*

D. E. Busch, U.S. Bureau of Reclamation, *The Bald Eagle and the Bureau of Reclamation in Kansas and Nebraska.*

W. R. Eddleman, University of Missouri, *Habitat characteristics and management of Swainson's Warbler on the fringe of its range.*

R. Casey, Rocky Mountain Biological Laboratory, *Energetic relationship between song and flight in sparrows.*

C. S. Adkisson, Virginia Polytechnic Institute and State University, *Ontogeny of flight calls in juvenile Pine Grosbeaks.*

R. D. Brown, University of North Carolina–Charlotte, *Vocal responses of the Indigo Bunting (*Passerina cyanea*) to playbacks of its own song.*

D. S. Raimist, Glassboro, N.J., *Vocalization patterns of endangered Palauan avifauna.*

T. Manolis, University of Colorado, *"Ornithological mystery" song, a generic song of* Rallus *species.*

R. C. Whitmore, West Virginia University, *Reclaimed surface mines as habitat islands in the eastern forest.*

James Tate, Jr., Atlantic-Richfield Co., Denver, *Raptor populations and coal mining in Campbell County, Wyoming.*

P. B. Wackenhut, West Virginia University, *The influence of vegetation structure on nesting success of Horned Larks on surface mines in West Virginia.*

D. C. Butler, Colorado State University, *Effects of overbrowsing on deciduous bird communities.*

L. B. McArthur, West Virginia University, *Avian community response to altered vegetation structure.*

T. Wray, II, West Virginia University, *Effects of vegetation on nesting success of Vesper Sparrows.*

R. L. Paterson, Virginia Polytechnic Institute and State University, *Distribution of old field birds along a vegetational gradient.*

F. B. Samson, U.S. Fish and Wildlife Service and University of Missouri–Columbia, *Avian distribution on tall grass prairie relicts.*

C. R. Preston, University of Arkansas–Fayetteville, *Ecological separation among color morphs of the Red-tailed Hawk (*Buteo jamaicensis*).*

B. Maurer, West Virginia University, *Foraging changes by some canopy-feeding birds in two eastern hardwood forests.*

K. L. Bildstein, Ohio State University, *Weather-dependent hunting of open habitat raptors wintering in south-central Ohio.*

P. Hicklin, Canadian Wildlife Service, Sackville, N.B., *Feeding ecology of migrant shorebirds in the Bay of Fundy.*

W. D. Rundle, University of Missouri–Columbia, *Foraging niches of some migrant shorebirds in Missouri.*

L. B. Best and E. J. Johnson, Iowa State University, *Factors affecting feeding frequency of Gray Catbird nestlings.*

G. E. Woolfenden, University of South Florida, *Feeding and dominance in the Florida Scrub Jay.*

M. M. Ninemeier, University of Nebraska–Lincoln, *Early sternal and tracheal development in* Grus canadensis *spp.*

P. E. Woods, Miami University, *Culmen ratios in a woodpecker guild.*

H. D. Pratt, Louisiana State University, *Systematics of Hawaiian "creepers."*

J. T. Paul, Jr., University of Delaware, *Morphological variation in island populations of the House Sparrow (*Passer domesticus*).*

E. J. Johnson, L. B. Best, and P. A. Heagy, Iowa State University, *Food sampling biases using the "ligature" technique.*

G. R. Batcheller, Oklahoma Coop. Wildl. Research Unit, Stillwater, *Time budgets of Blue Jays in pecan orchards in central Oklahoma.*

J. S. Munzinger, Briar Cliff College, Iowa, *Energetics of Black-capped and Carolina chickadees (*Parus atricapillus *and* P. carolinensis*).*

R. B. Frederick, Iowa State University, *Energetics of fall-migrating Lesser Snow Geese at DeSoto National Wildlife Refuge.*

R. Packard and J. L. Zimmerman, Grinnell College and Kansas State University, *Biggest is not best in male Dickcissels.*

P. W. Brown and M. A. Brown, Iowa State University, *White-winged Scoter breeding biology.*

D. H. White, C. A. Mitchell, and E. Cromartie, U.S. Fish and Wildlife Service, Victoria.

Texas and Laurel, Maryland, *Breeding success of Roseate Spoonbills in Nueces Bay. Texas, 1978.*

P. E. Lowther, University of Kansas, *Growth and dispersal of nestling House Sparrows: sexual differences.*

C. L. Cink, Baker University, *Food availability and dispersal in House Sparrows.*

H. R. Postovit, North Dakota State University, *A survey of Spotted Owls in Northwest Washington forests.*

N. L. Ford, St. John's University, *Extraterritorial activities of male Yellow Warblers.*

S. M. Smith, Adelphi University, *Responses of naive birds to warning coloration.*

E. P. Mallory, Dartmouth College, *Behavior and ecology of Whimbrels (*Numenius phaeopus*) wintering on mangrove flats along the Bay of Panama.*

H. S. Lapham, Laboratory of Ornithology, Ithaca, N.Y., *The Song Sparrow—a distraction display imitative of young.*

R. M. Zammuto and E. C. Franks, University of Arkansas, *Environmental effects on the roosting behavior of Chimney Swifts.*

S. F. Elston, Northern Illinois University, *Effects of intraspecific kleptoparasitism on breeding Ring-billed Gulls.*

B. M. Gottfried, College of St. Catherine, *Anti-predator aggression in birds nesting in old-field habitat.*

J. H. Rappole, University of Minnesota, *Intra- and intersexual competition in migratory passerine birds during the non-breeding season.*

K. O. Horner, Hollins College, *Passerine migration patterns and post glacial invasion of the Palaearctic.*

R. E. Babcock, Bronson, Michigan, *An historical account of the avifauna of Branch County, Michigan, 1830–1910.*

SYMPOSIUM ON THE BIOLOGY OF BIRDS WITH RESTRICTED RANGES

Jon C. Barlow, Royal Ontario Museum, Introduction.

M. H. Clench (read by G. E. Woolfenden), Carnegie Museum, Pittsburgh, *Kirtland's Warbler: a relict species.*

W. M. Pulich, University of Dallas, *The Golden-cheeked Warbler—its restricted range.*

Jon C. Barlow and R. I. Orenstein, Royal Ontario Museum and University of Michigan, *Evolutionary features of the behavior of* Vireo osburni.

T. R. Anderson, McKendree College, *The role of competition in limiting the distribution of the European Tree Sparrow in North America.*

J. A. Jackson, Mississippi State University, *Adaptations for survival in woodpecker species with small ranges.*

W. D. Graul, Colorado Division of Wildlife, *The Mountain Plover: coping with a restricted, harsh environment.*

R. S. Sharpe, University of Nebraska-Omaha, *The Lesser Prairie Chicken: grouse of the Dustbowl.*

The following persons chaired sections of the scientific program: A. S. Gaunt, R. C. Banks, R. D. Brown, J. C. Barlow, R. C. Whitmore, J. L. Tate, Jr., G. E. Woolfenden, H. B. Tordoff, S. Munzinger, H. Lapham, S. Smith, S. A. Gauthreaux.

ATTENDANCE

ALASKA: *Anchorage*, Larry L. Hood.

ARKANSAS: *Fayetteville*, Joan Ballam, Fred Burnside, Douglas A. James, Joe Lockerd, Mercedes C. Mondecar, Charles R. Preston; *Little Rock*, Robin R. Rhinehart.

COLORADO: *Boulder*, Richard M. Casey, Jeanne Conroy, Alex Cruz, Timothy Manolis; *Fort Collins*, Clait E. Braun, D. C. Butler, Dale Hein, Edward Hollowed, Richard Pillmore; *Golden*, James Tate; *Northglen*, Walter D. Graul.

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NEW BRUNSWICK: *Sackville*, P. W. Hicklin.

ONTARIO: *Toronto*, Jon C. Barlow, Margaret May.

SASKATCHEWAN: *Saskatoon*, William J. Maher.

ADDRESS NOT PROVIDED: Bill Clark, Marian Doyle, Dale Herrman, Mark Parts, Herbert Hodges, Mark Pfeffer, Jeff Short.

Erratum.—Back cover, Contents, General Notes of June 1979 (Vol. 91, No. 2) add "Interspecific use of Sandhill Crane nests" by Carroll D. Littlefield, p. 323.

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The Wilson Bulletin

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THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

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Young Everglade Kites *(Rostrhamus sociabilis)* at the nest.

THE WILSON BULLETIN
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Wilson Bull., 91(4), 1979, pp. 495–511

STATUS OF THE EVERGLADE KITE IN FLORIDA—1968–1978

PAUL W. SYKES, JR.

The Florida Everglade Kite (*Rostrhamus sociabilis plumbeus*) was discovered on 29 April 1844, by Edward Harris (1844), who secured an immature male (ANSP 1942, Acad. Nat. Sci. Philadelphia) near the headwaters of the Miami River, in what is now Dade County, Florida. Recently, Amadon (1975) reviewed the taxonomy of *R. sociabilis* and concluded that *R. s. levis* of Cuba is not subspecifically distinct from *plumbeus* of Florida. *R. sociabilis* is still common in Cuba (Schwartz and Klinikowski 1963, Garrido and Montana 1975), but the Florida population of the species has been threatened with extinction for several decades.

There were no reliable counts or population estimates of the Everglade Kite in Florida before the 1920's, probably because of the inaccessibility of the terrain within the range of the species there. Howell (1932:169) provided a general idea of kite abundance when he mentioned "scattered flocks of a hundred or more birds frequently being found in a limited area." Sprunt (1945), the first to report a serious population decline, thought that only 50–100 kites were left in 1945. He had observed a steady decline at Lake Okeechobee and disappearance of the species from the headwaters of the St. Johns River. In 1950 Sprunt (1950) estimated there were no more than 100, and probably fewer than 60; and in 1954 no more than 50–75 (Sprunt 1954). In 1963 Sprunt (1963) estimated ca. 6 birds remaining, based on sightings at Lake Okeechobee and the Loxahatchee National Wildlife Refuge. Stieglitz and Thompson (1967) reported 8 kites in 1963 on the Loxahatchee Refuge, 17 on the refuge and 2 at Lake Okeechobee in 1964, 8 in Conservation Area 2A (CA2A) and 2 at Lake Okeechobee in 1965, and 21 in CA2A in 1966.

The Florida Everglade Kite was declared endangered in 1966 by the Committee on Rare and Endangered Wildlife Species, and in 1967 the present study was initiated as part of the Endangered Wildlife Research

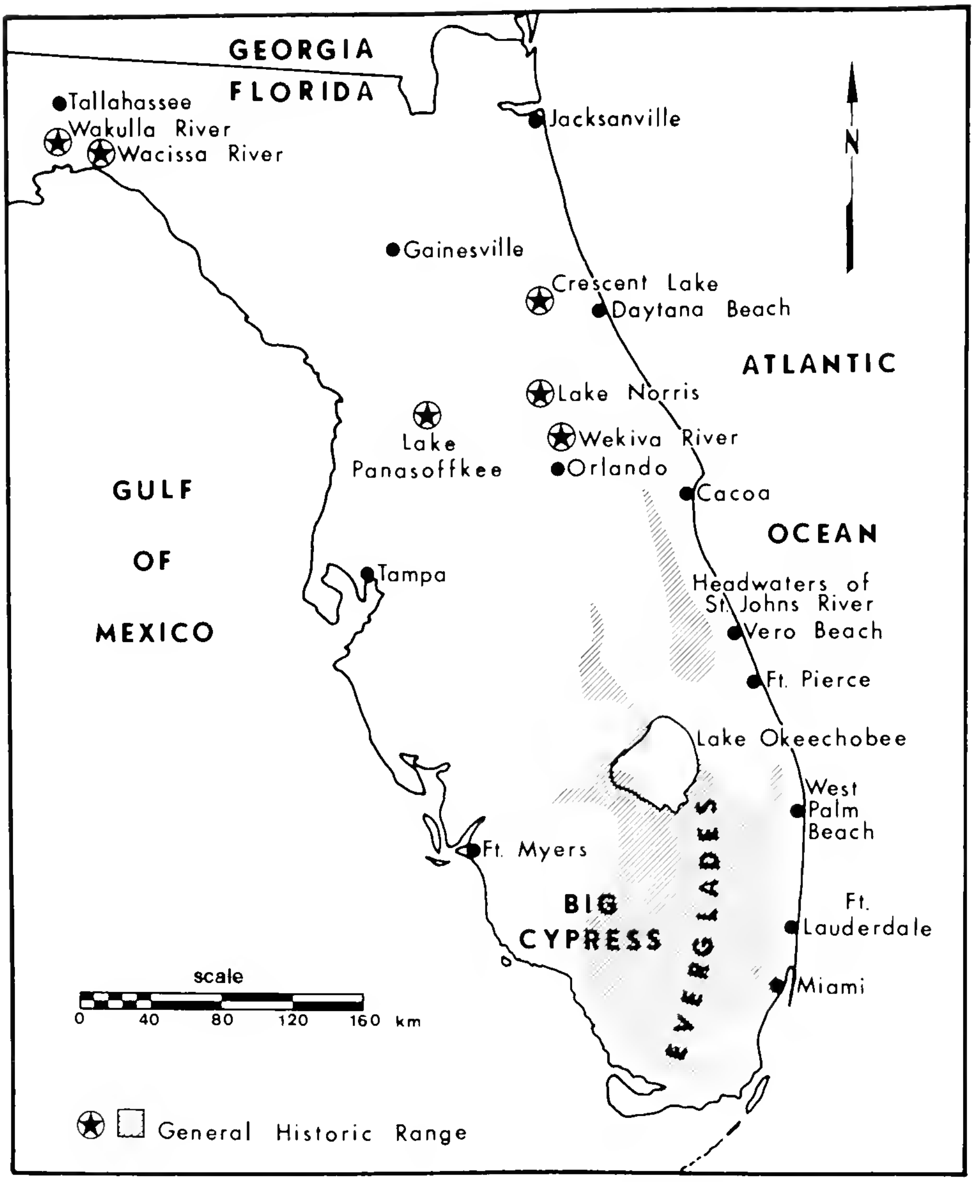

FIG. 1. The historic range of the Everglade Kite in Florida.

Program of the Fish and Wildlife Service. In initial studies in the fall of 1967 I counted a minimum of 47 birds: 39 in CA2A, 6 in CA3A, and 2 at Lake Okeechobee, and in 1968 I estimated there were at least 50 to 70 individuals in southern Florida. This paper reviews the recent history and general habitat requirements of the species and some associated problems. The results of color-marking birds of known age, censusing, and findings on age of sexual maturity, population movements, productivity, longevity, and population status are presented in some detail.

STUDY AREA AND METHODS

Range in Florida.—The historic range of the Everglade Kite (Howell 1932) is shown in Fig. 1. At present the kite is confined principally to the headwaters of the St. Johns River (man-made impoundments in Indian River and St. Lucie counties) and the west side of Lake

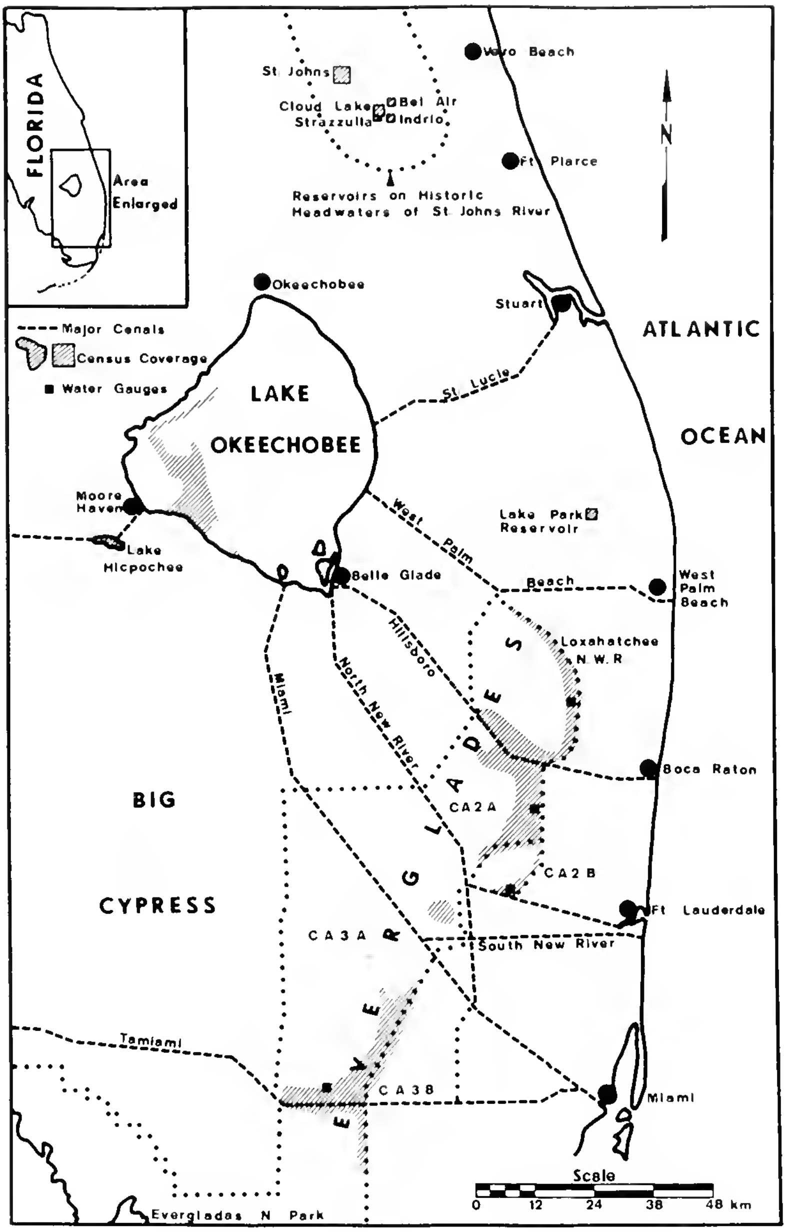

FIG. 2. Present range and areas in Florida censused 1969–1978. The 5 reservoirs on the headwaters of the St. Johns River and the Lake Park Reservoir are not to scale or shown in their true configurations.

Okeechobee southward through the Everglades (Loxahatchee National Wildlife Refuge, Conservation Areas 2A, 2B, 3A, and 3B, and the northern part of Everglades National Park) (Fig. 2). Wandering individuals are sometimes seen elsewhere within the former range and occasionally beyond it.

General habitat requirements.—This raptor generally inhabits large freshwater marshes with unobstructed air space and low vegetation. There are usually few tree islands in wetlands occupied by the kite, although there are generally scattered shrubs or small, low trees, mainly willow (*Salix caroliniana*), dahoon holly (*Ilex cassine*), wax myrtle (*Myrica cerifera*), pond apple (*Annona glabra*), and bald cypress (*Taxodium distichum*), which serve as perches and nesting sites. The kite hunts mainly over the extensive, shallow (water depth 0.2–1.3 m) sloughs of white waterlily (*Nymphaea odorata*) and wet prairies or flats of spikerush (*Eleocharis elongata* and *E. cellulosa*) that retain some surface water through the dry season in most years (Loveless 1959). Such areas occur in extensive stands of sawgrass (*Cladium jamaicensis*) or cattails (*Typha domingensis* and *T. angustifolia*) or on flat river courses and margins of large shallow lakes. Continuous flooding of a marsh for a period of several years is needed to develop and sustain an adequate supply of the apple snail (*Pomacea paludosa*). This snail is normally the only food taken by kites in Florida (Sykes and Kale 1974). Apple snails remain active only when the marsh is inundated. If the marsh dries up, snail numbers are drastically reduced by predation and the survivors burrow into the bottom and become unavailable to kites.

Originally, more than a fourth of peninsular Florida was covered with surface water much of each year (Tebeau 1971). The initiation of drainage in the peninsula was in the 1881–1894 period. Construction of the major works began in 1905 and has continued intermittently to the present (Parker et al. 1955, Anon. 1957, Tebeau 1971, Johnson 1974). This widespread drainage has permanently lowered the water table as much as 1.5 m in some places in southern Florida (Parker 1951, Klein et al. 1974) and up to 2.1 m on the headwaters of the St. Johns River. Large tracts of freshwater marsh have been eliminated and much of what remains has been modified so that it is no longer suitable habitat for kites.

From 1910 until 1950, little effort was made to control runoff of fresh water from the Everglades through major canals emptying into the tidal estuaries of the southeastern Atlantic coast. In the late 1940's the U.S. Army Corps of Engineers began development of the Central and Southern Florida Flood Control Project and in 1949 the Central and Southern Florida Flood Control District (now the South Florida Water Management District) was created. With the construction of that project and formation of the district, the flow of water to the sea was controlled and 3 conservation areas were created in the Everglades ecosystem to store water and reduce flooding in developed coastal areas (Parker et al. 1955, Tebeau 1971, Leach et al. 1972, and Klein et al. 1974). The creation of the conservation areas has secondarily been of great benefit to the kite population by flooding parts, or all of the area for several years. However, because of demands for fresh water for agricultural, municipal and industrial uses, there is not enough to maintain large areas of flooded habitat suitable for kites on a long term basis. Prior to the creation of the conservation areas the Everglades was dry much of the time, and man-created fires were frequent and widespread (Robertson 1953, Hofstetter 1974).

In addition to loss of habitat from drainage, large areas of marsh are heavily infested with water hyacinth (*Eichhornia crassipes*). This plant was introduced into Florida on the St. Johns River in 1884 (House Document No. 37, 85th Congress 1957) and was well established in the southern part of the state by the 1920's (Johnson 1974). If uncontrolled, the water hyacinth propagates rapidly and forms dense blankets of vegetation. Since kites hunt visually, areas thus obscured cannot be used by them.

Methods.—I conducted preliminary investigations from the fall of 1967 through the summer of 1969 to locate kite habitat in Florida, to determine the best time of year to census, and to become familiar with the kites behavior and activities. The censuses started in 1969 were the first organized effort to census kites in most of its present habitat. Because the bird is gregarious, relatively approachable and conspicuous, I censused by direct counting (census and count as used in this paper are synonyms). With an airboat I ran standardized transects through the available habitat, and counted birds arriving at night roosts in late afternoon, and from a vehicle on the levee and road system in, or adjacent to kite habitat. Approximately 85–90% of the time in the field was spent in airboats; the remainder in vehicles on the levee system.

Replicate censuses were made on the transects at each locality in 1976 and the results

TABLE 1

NUMBERS, PERCENTAGE OF FLEDGED YOUNG, AND SUBSEQUENT SIGHTINGS OF EVERGLADE KITE NESTLINGS BANDED 1968–1976

	Banded		Observed after banding			
			Two months or more		One year or more	
Year	Total	Percent of known fledged young	Number	Percent[1]	Number	Percent[1]
1968	15	63	6	40	3	20
1969	7	54	3	43	2	29
1970	9	75	2	22	2	22
1971[2]	0	—	—	—	—	—
1972	3	43	0	0	0	0
1973	13	45	1	8	1	8
1974	10	91	3	30	3	30
1975	2	6	1	50	0	0
1976	5	17	0	0	0	0
Total	64	—	16	—	11	—
Mean/year[3]	8.0	49	2.0	24	1.4	14

[1] Percent of those banded for given year.

[2] Year of drought; no nesting activity observed.

[3] Excluding 1971.

(total for the first day at all localities compared with total for the second day at same localities) differed numerically by 8 birds. Duplicate counts were not made at roost sites. I recorded kites by locality, time and population category and completed each census within a 10–14 day period. I recognized 3 population categories by plumage characteristics: (1) gray–males 3 years and older; (2) brown–all females and first and second year males; and (3) unknown–individuals too poorly seen to assign to either of the above groups.

In the airboat I used, seats were mounted 1.5 m above the bottom of the boat, and with the marsh flooded, the observer has an unobstructed view. The noise of the engine flushed kites at distances up to 100–150 m. The birds would rise, fly about for several minutes, and then settle again into the marsh, allowing sufficient time to check each individual. Censusing from an airplane and helicopter proved unsatisfactory.

Areas covered on the annual censuses (Fig. 2) included: 5 reservoirs on the historic headwaters of the St. Johns River (St. Johns in Indian River County; and Cloud Lake, Strazzulla, Bel Air, and Indrio in St. Lucie County), the Savannas at Ft. Pierce (St. Lucie County), flooded portion of the marsh on the west side of Lake Okeechobee, Lake Hicpochee, Lake Park Reservoir (Palm Beach County) in the Loxahatchee Slough (=Marsh), eastern and southern Loxahatchee National Wildlife Refuse (=Conservation Area 1), eastern and southern CA2A, northern and southern CA2B, eastern and southern CA3A, western CA3B, and northern Everglades National Park.

Nests were found by 2 methods: (1) searching the marsh where birds were present, and (2) watching the activities of individuals. The latter technique was the more efficient and all nests in a given area could be found in this manner. Because most adults were not banded it was not possible to conclusively distinguish between initial and renesting attempts. A new structure is built at each nesting. The birds nest in loose colonies and nesting territories are

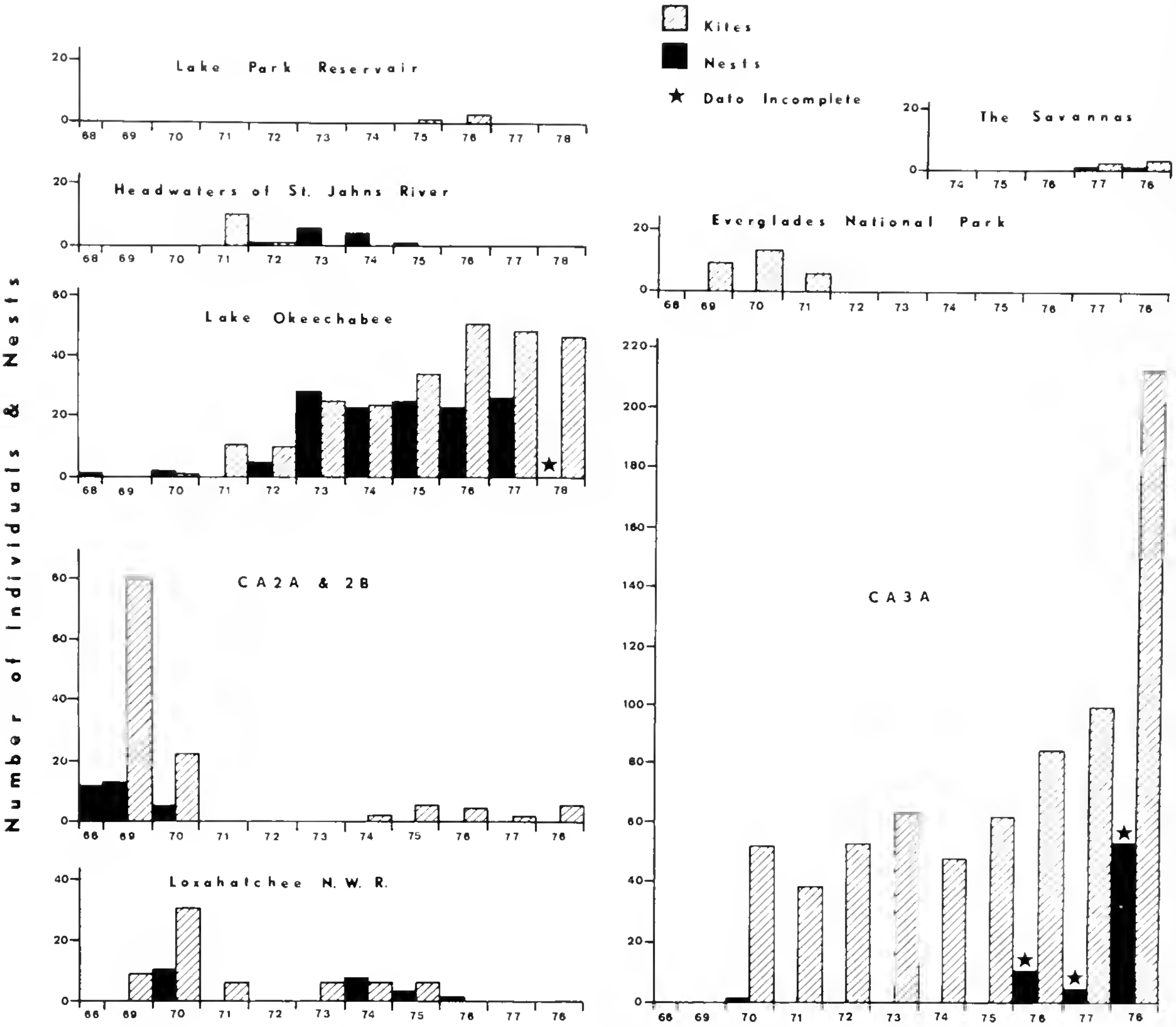

FIG. 3. Distribution of Everglade Kite nesting (1968–1978) and wintering (1969–1978) (based on census Nov.–Dec.) in Florida.

not established. A successful nest was one from which 1 or more young were fledged (take first true flight). I did not study kite reproduction after 1976.

Nestlings were banded at 20–30 days of age with USFWS aluminum bands in combination with colored plastic bands. Sixty-four nestling kites were color-banded from 1968 through 1976 (Table 1). This is 40% of the young known to have fledged during that period ($\bar{x}$ = 9.0 banded per year excluding 1971 when no young were produced). No attempt was made to band adults. Linear regression was used to test for population increases over time.

RESULTS

Age at sexual maturity.—Male kite nestlings obtained from the Province of Buenos Aires, Argentina, and raised at the Patuxent Wildlife Research Center, Laurel, Maryland, attained subadult plumage in their third year and adult plumage in the fourth (Glen Smart, pers. comm.). Haverschmidt (1970) reported subadult plumaged *R. s. sociabilis* breeding in Surinam, but did not know the ages of the individuals involved. Allan Brooks collected a breeding *R. s. plumbeus* subadult male (MVZ 99638) at West

Palm Beach on 19 March 1921. In Florida I found males in subadult plumage breeding in April and May 1968, and February and March 1970; and Rod Chandler (pers. comm.) found one breeding in February 1973. A female I color-banded as a nestling on 23 March 1970, was nesting in June 1973. Thus, at least some individuals breed at the age of 3 years, and possibly younger.

Population movements.—This species roosts gregariously, nests in loose colonies, and individuals usually associate freely during daily activities (Howell 1932, Haverschmidt 1954, 1970; Brown and Amadon 1968). However, Snyder and Snyder (1970) described several kites defending temporary hunting territories in an area of the Everglades with a high snail population, a previously undescribed phenomenon for the species. Since 1968 I have witnessed intraspecific aggression over a hunting territory only once and that between 2 males in CA3A.

My field work, beginning in 1967, has shown that kites are nomadic in Florida. Since widespread water manipulation has affected their food supply, kites must be nomadic to survive. Wintering and nesting activities of the species are shown for 8 major areas used by kites in recent years (Fig. 3). From 1968 through 1970, CA2A and CA2B were used by kites, but little since then. In contrast, Lake Okeechobee, lightly used from 1968 through 1971, has had heavy use since then and is currently a major breeding site. No kites were found in CA3A in 1968 and 1969, but it has been the primary wintering ground for the Florida population since then and the major nesting area since the mid 1970's. Loxahatchee Refuge has had only sporadic use since routine observations began in the 1950's.

Observations of marked known-age kites clearly demonstrate that the change in the pattern of use of the 8 major areas is not simply attributable to rapid fluctuations in sedentary populations. For example, a female I banded in eastern CA2A in March 1968 was seen on the west side of Lake Okeechobee in the spring of 1976 (Rod Chandler, pers. comm.), and a female banded in CA2A in 1969 was seen in April 1974 on the St. Johns Reservoir, in November 1975 in CA2A, in March 1976 on Loxahatchee Refuge, and in December 1976 in CA2A. Another female banded on the refuge in April 1970 was seen in CA3A in December 1970, at its nest at Lake Okeechobee in June 1973, and at its nest at Loxahatchee Refuge in March 1974, and in CA3A in November 1974. A bird of unknown sex banded on Loxahatchee Refuge in April 1970 was seen in CA3A in December 1970, and at Lake Okeechobee in December 1971.

The nomadic behavior exhibited by this kite in recent years, probably represents a normal response to changes in water levels and food availability. Howell (1932) reported that a search of Loxahatchee Slough in 1923 failed to reveal a single kite, although the species bred there in abundance in 1921. Very likely the birds had simply moved elsewhere.

TABLE 2
EVERGLADE KITE REPRODUCTION 1968–1976

Year	Nests					Young	
	Observed	Successful	Failed	Results unknown	Percent successful	Total number fledged	Fledged per successful nest[1]
1968	13	11	2	0	84.6	24	2.2
1969	13	8	2	3	80.0	13	1.6
1970	19	8	10	1	44.4	12	1.5
1971[2]	0	—	—	—	—	0	—
1972	6	3	3	0	50.0	7	2.3
1973	34	12	22	0	35.3	29	2.4
1974	35	6	29	0	17.1	11	1.8
1975	29	14	15	0	48.3	35	2.5
1976	34	22	8	4	73.3	30	1.4
Totals	183	84	91	8	48.0	161	1.9
Mean/year[3]	22.9	10.5	11.4	1.0	54.1	20.1	2.0
SE	4.07	2.05	3.53	—	8.28	3.74	0.15

[1] Only those nests in which the exact number of young fledged is known were used to derive these figures.
[2] Severe drought conditions throughout peninsular Florida; no nesting attempts observed.
[3] Excluding 1971.

Sex and age ratios.—The sex ratio in the Florida kite population is unknown. Adult kites are sexually dimorphic in plumage and females average slightly larger than males (Friedmann 1950), but the size difference is impossible to detect in the field. Also, ages cannot be determined under field conditions. The plumages of adult females and all immatures are similar. Immatures can be distinguished from adult females at close range by iris color (carmine in adult females, brown in immatures). The time required for the eye color change is not known. The plumage of older adult females tends to darken with some slaty-black on the crown, nape and upper back, but most of the plumage retains an overall brownish cast. This latter feature can be seen under field conditions and enables one to distinguish old females from 3-year old males. The whitish throat is retained but reduced in size. The 3-year old males have more gray throughout the plumage than the darkest of the adult females. For the above reasons, the age and sex classes that can be determined consistently in the field are gray adult and subadult males, and brown females and immature males. There is no accurate, reliable method of sexing kites of these age groups in the hand.

Natality.—I estimated about 70–80% of the nests were found each year from 1968 through 1974. Each nest was observed at varying intervals until the young fledged or the nest failed. From 1968 through 1976, breeding

TABLE 3

EVERGLADE KITE NESTING SUCCESS BY LOCALITY IN FLORIDA 1968–1976

		Nests			
			Successful		
Year		Observed	Number	Percent[1]	Percent of total[2]
1968	Lake Okeechobee	1	1	100	9
	CA2A	12	10	83	91
1969	CA2A	13	8	80	100
			+3 unknown	—	—
1970	Lake Okeechobee	2	1	50	12.5
	Loxahatchee N.W.R.	11	5	50	62.5
			+1 unknown		
	CA2A	4	1	33	12.5
			+1 unknown	—	—
	CA2B	1	0	0	0
	CA3A	1	1	100	12.5
1971	—	0	—	—	—
1972	Headwaters St. Johns River	1	1	100	33
	Lake Okeechobee	5	2	40	66
1973	Headwaters St. Johns River	6	3	50	25
	Lake Okeechobee	28	9	32	75
1974	Headwaters St. Johns River	4	0	0	0
	Lake Okeechobee	23	6	26	100
	Loxahatchee N.W.R.	8	0	0	0
1975	Headwaters St. Johns River	1	1	100	7
	Lake Okeechobee	25	13	52	93
	Loxahatchee N.W.R.	3	0	0	0
1976	Lake Okeechobee	23	18	78	82
	Loxahatchee N.W.R.	1	1 unknown	—	—
	CA3A	10	4	40	18

[1] Nests for which results are unknown are excluded from the calculations.

[2] Same as 1.

success was determined for 175 nests with a success rate of 48.0% (Table 2). There was a statistically significant increase ($r = 0.685$, $P < 0.05$) in the number of nests observed (excluding 1971) (Table 2), but no significant change in nesting success, failure, percent successful, number fledged, or number fledged per successful nest for 1968–1976. During this period 161 young were known to have fledged, $\bar{x} = 20.1$ young per year, or 1.9

(=2.0 per year) per successful nest (N = 84). No young were produced in the drought-year 1971 and only 7 young were known to fledge in 1972. Among pairs in which at least 1 member was subadult (3-year old birds; 6 males and 1 female), 4 nests (57%) were successful.

Nesting success by localities is given in Table 3. In 1968 and 1969 most breeding activity was in the eastern part of CA2A; and in 1970 it shifted to the eastern edge of Loxahatchee N.W.R. From the 1971 drought through 1975, nesting has occurred primarily on the southwest side of Lake Okeechobee, and 1976 through 1978 on the lake and in southeastern CA3A. Nesting results from year to year have been variable (Tables 2 and 3) with the most successful nesting observed in CA2A in 1968, when 84.6% of the nests fledged young. During the period 1973–1976 the greatest nesting success was at Lake Okeechobee.

Mortality.—I could not measure kite mortality (excluding nestlings) for the period 1969 through 1978 as not enough birds were marked. Nestling mortality for the 1968–1974 period (omitting 1971) was 41% (96 young fledged from 163 eggs that hatched). Mortality was attributable to parasites, predators, weather, and accidents (Sykes, unpubl.). Although causes of natural mortality among all other age classes are undocumented, disease, predation and accidents undoubtedly are involved, and some individuals probably starved in drier years. Learning to hunt for snails, and to do so proficiently, appears difficult for young kites and many probably do not survive that stage of development. For example, on several occasions I observed young, recently out of the nest and not attended by parents, with the wing, tail and ventral feathers wet (when it had not been raining) and with most rectrices and several primaries and secondaries in disarray. If this plumage condition were to occur frequently, or last for several days during the time hunting skills were being perfected an individual might be rendered flightless and hence not survive. Older birds hold the wings and tail high when hunting and seldom touch the emergent vegetation or get the remiges and rectrices wet when capturing their prey.

Of the 64 color-banded nestlings (Table 1), 16 (25%) were subsequently seen 2 or more months and 11 (17.2%) 1 or more years after they were banded. However, since not all kites were examined for bands in the wild these sightings cannot be converted into survival statistics.

Illegal shooting is still a problem, particularly during the waterfowl hunting season (in southern Florida this is generally from late November to 20 January). The slow, low-level flight and lack of fear of man make kites easy targets for the uninformed or the intentional violator. Sprunt (1945) reported this problem at Lake Okeechobee in the 1940's. More recently I have 2 records of kites that were killed by shooting in 1971 (J. W. Dineen, R. A. Martz, and B. G. Murray, Jr., pers. comm.), and I have observed

TABLE 4
ANNUAL EVERGLADE KITE CENSUSES 1969–1978

Year	Population categories						Number of individuals
	Gray birds[1]		Brown birds[2]		Unknowns		
	Number	Percent[3]	Number	Percent	Number	Percent	
1969	20	20	76	78	2	2	98
1970	21	18	87	72	12	10	120
1971	23	32	49	68	0	0	72
1972	23	35	36	55	6	9	65
1973	41	43	52	55	2	2	95
1974	38	47	33	41	10	12	81
1975	47	43	52	47	11	10	110
1976	52	37	76	53	14	10	142
1977	58	38	91	60	3	2	152
1978	66	25	187	70	14	5	267
Mean/year	38.9	—	73.9	—	7.4	—	120.2
SE	5.30	—	14.12	—	1.71	—	18.61

[1] Adult and subadult males.
[2] Females and immature males.
[3] Percentage of total count.

kites during and after each waterfowl hunting season with flight feathers that appeared to have been damaged by shot. Such damage is evident by broken rachises still attached, missing distal portions of the remiges or rectrices, or holes in vanes of the feathers. How many are lost to illegal shooting and that go undetected is unknown, but with such a small population each loss is significant.

Longevity.—Nine of the surviving *R. s. sociabilis* that were taken as nestlings in northern Argentina (in December 1965 and 1966, and January 1967), and held in captivity at Patuxent Wildlife Research Center, are 12 and 13 years old. The females are still in good egg production and the males are producing viable sperm (George Gee, pers. comm.). A female banded on 8 October 1969, in CA2A was seen on 13 December 1976, at that same locality; a female (first of the species ever banded), banded in the same general area as the preceding on 21 March 1968, was seen at Lake Okeechobee in April and May 1976 (Rod Chandler pers. comm.); a female banded 18 April 1969, in CA2A was seen on 21 November 1977, in CA3A; and a kite banded 7 April 1968, in CA2A was seen at Lake Okeechobee on 23 February 1977 (Rod Chandler, pers. comm.). These birds were 7.2, 8.1, 8.6, and 8.8 years old, respectively. The life expectancy of the Everglade Kite in the wild is not known, but they seem relatively long lived, based upon the above observations. Some individuals probably live 10 years and perhaps much longer.

TABLE 5

SAMPLE OF ANNUAL CENSUSES CHECKED FOR BANDS AND THE PERCENTAGE OF BANDED BIRDS FOUND WITHIN EACH POPULATION CATEGORY

Year	Percent of census total checked for bands	Banded birds in checked sample of each population component			
		Gray birds[1]		Brown birds[2]	
		Number	Percent[3]	Number	Percent
1969	27	5	19	22	81
1970	17	7	33	14	67
1971	25	7	38	11	61
1972[4]	1	0	0	1	100
1973	10	4	40	6	60
1974	29	8	33	16	67
1975	20	5	22	17	77
1976	23	7	21	26	79
1977	15	5	21	18	78
1978	0	—	—	—	—
Mean/year	17	4.8	—	13.1	—

[1] Adult and subadult males.
[2] Females and immature males.
[3] Percentage found to be banded among the sample checked.
[4] The data are incomplete because visibility was too poor to check for bands the day 81% of the birds were observed.

Population status.—Ten censuses were conducted from mid-November to mid-December from 1969 through 1978. The minimum numbers of individuals observed are given in Table 4. For the 10-year period $\bar{x} = 120.2$, with a low of 65 in 1972 and a high of 267 in 1978. I recorded from 2.1 to 6.2 birds/h of effort on the transects; $\bar{x} = 3.1$ based on 38.2 h/census ($\bar{x}$).

Banded birds that were checked for bands on the annual censuses are summarized in Table 5. Because of the problem of keeping track of individuals in the course of censusing, only an average of 17% (4.8% gray, 14.1% brown) have been inspected for bands on the censuses.

The kite population increased to a high of 120 in 1970 (Fig. 4) following a series of wet years with high water levels. In 1971 southern Florida experienced a severe drought and most of the freshwater marshes dried up, resulting in a sharp decrease in the kite population that continued through 1972. Since the 1971–1972 period, the number of kites has increased, with a minor decline in 1974 (Fig. 4). The decrease in 1974 is attributed to a low recruitment rate (Tables 2 and 3) resulting from low water conditions at Lake Okeechobee, CA2A, and CA3A, and complete nesting failure at Loxahatchee. From 1974 through 1978 the population has increased significantly ($r = 0.92$, $P < 0.025$) (Fig. 4). This latter in-

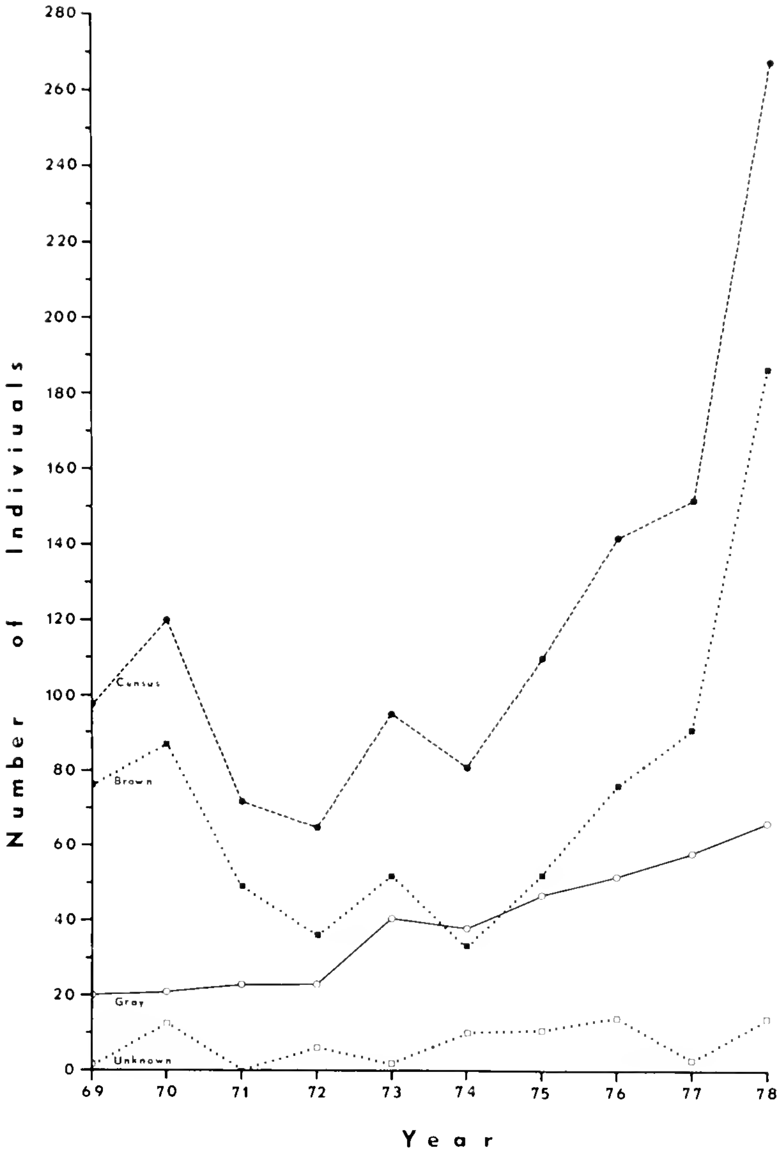

FIG. 4. Population categories of the Everglade Kite in Florida on annual censuses 1969–1978.

crease is apparently the result of favorable water conditions and an abundance of snails in certain portions of the marsh on the west side of Lake Okeechobee and the southeastern edge of CA3A.

The number of brown kites has roughly paralleled the census totals (Fig. 4), whereas the gray birds (breeding males) have shown a constant slow increase irrespective of the fluctuating census results, except in 1974. This steady increase in the number of gray birds (Table 4) is highly significant ($r = 0.97$, $P < 0.001$). There is no significant trend among the brown birds because reproductive success is so variable, and adult females cannot readily be distinguished from birds up to 2 years old. Since 1974 the ratio of brown to gray birds appears normal. The number of brown kites has ranged from 187 in 1978 to 33 in 1974 ($\bar{x}$ = 73.9) (Table 4). Taking the low of 33 as an accurate figure, the brown categories of the population had increased by 566% by the end of 1978. The ratio of brown to gray in 1978 was approximately 1.8:1, excluding the 14 birds in the unknown category.

The number of adult and subadult males increased from 20–66 from 1969 through 1978 (Table 4 and Fig. 4), or 330%. Only 2% of all gray-plumaged birds recorded over the 10-year period were subadult males. In 1978, males 3 or more years old comprised 25% of the census total.

DISCUSSION

Previous estimates of the kite population in Florida are not directly comparable to the results of my study because I censused more kite habitat and used different techniques. I censused in November and December because kites in Florida congregate more at this time than in other months and water levels are high enough to permit access to all regularly censused marshes. Censusing in other months gave less reliable estimates of population size because of dispersal, breeding activities and lower water levels or a combination of these. Low water not only makes access more difficult but also reduces visibility as the height of the marsh vegetation is relatively constant, but the height of the observer on the airboat and observational effectiveness increases or decreases in relation to water level.

The population of Everglade Kites was probably never as low as Sprunt's (1963) estimate of about 6 birds in the early 1960's, but the number could have been as low as 20–25 individuals based upon the data presented by Stieglitz and Thompson (1967). The higher totals from censuses may be more accurate than the lows because they were recorded when the kites were more concentrated, the lows when they were more dispersed. Although counts at night roosts were not incorporated into the censuses until 1973, results of censuses for 1969–1972 and 1973–1978 are believed to be reasonably comparable.

The age categories of the population have probably not been counted with equal accuracy because immatures tend to wander farther from the main population than adults, and the amount of dispersal differs from year to year. This could explain the variation in the number of brown birds in different years. This is further complicated by the number of kites recorded as unknowns.

Each year, following breeding, some birds disperse, but during the drought of 1971 they were scattered more widely than usual over the entire Florida peninsula. The reduced food supply resulting from dry conditions apparently raised the mortality rate. In 1971 there was no recruitment to the population from reproduction and when the census was taken only 72 individuals could be found. Although dispersal might have affected the actual number of birds seen, it was obvious that the population had decreased. In 1972 nesting attempts were at least 60% below the 1968–1970 period, and only 65 individuals were recorded on the census. Dry conditions prevailed in 1974 and there was a corresponding decrease in the kite population (Fig. 4). There is no evidence to indicate movement between the Florida population and that in Cuba, but whether such movements occur remains to be determined.

The Everglade Kite population in Florida (since 1974) and the number of gray birds (1969–1978) have shown a strong and highly significant ($r = 0.92$, $P < 0.025$ and $r = 0.97$, $P < 0.001$ respectively) increase during a series of years with high water levels. The increase in gray birds has resulted in more nesting (Table 2 and Fig. 3). If favorable water conditions continue in the major areas, this population increase is expected to continue.

Censuses for the 10-year period revealed a low of 65 birds in 1972 and a high of 267 in 1978. This represents the greatest number of kites in Florida since the 1920's or 1930's. Although the kite population has adjusted to habitat loss since completion of the first drainage works, most areas now used by kites are committed to other water management programs, meaning less water in the future. It is vital to the survival of the kite population in Florida that habitat units be developed and managed. Such units could supplement already scarce habitat and insure sufficient resources to support the kite population through critical periods of low water.

SUMMARY

The population status of the Everglade Kite (*Rostrhamus sociabilis plumbeus*) was studied in Florida from 1968 through 1978. Sixty-four nestlings (40% of known fledged young) were leg-banded with unique color combinations, and of these, 17.2% were seen 1 or more years after they were banded. Kites were capable of breeding at 3 years of age or possibly younger. The population was nomadic; its sex ratio unknown. From 1968 through 1976 breeding success was determined for 175 nests, of which 48% were successful: 161 young were fledged, $\bar{x} = 20.1$ per year, or 1.9 per successful nest (N = 84). The percentage of successful nests ranged from 17.1 (N = 35) in 1974 to 84.6 (N = 13) in 1968 ($\bar{x} = 54.1$ per year). From 1968 through 1976 there was a significant increase ($r = 0.685$, $P < 0.05$) in the number of nests observed (excluding 1971, and reproduction was not studied in 1977 and 1978). The mortality rate for young in the nest was 41%. Some individuals live for at least 8+ years. The mean number of kites for 10 annual censuses was 120.2 with a range of 65 (1972) to 267 (1978). The severe drought of 1971 resulted in a significant decrease in the population for that year and 1972, with no nesting attempts being observed in the dry year. From 1974 through 1978 the population increased significantly ($r = 0.92$, $P < 0.025$), apparently the result of favorable water conditions and increased food supply. The loss of suitable habitat is the major problem facing

the species in Florida. A high water level is essential, as this affects food supply and its availability, as well as nesting success.

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COLOR PLATE

The color plate Frontispiece of young Everglade Kites at the nest has been made possible by an endowment established by Dr. George M. Sutton.

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RECENT WOOD STORK POPULATION TRENDS IN THE UNITED STATES

JOHN C. OGDEN AND STEPHEN A. NESBITT

The population of Wood Storks (*Mycteria americana*) resident in the United States occurs on the coastal plain of the Gulf of Mexico and the southern Atlantic states. Historically, storks nested in all coastal states from Texas to South Carolina (Bent 1926, Cone and Hall 1970, Dusi and Dusi 1968, Howell 1932, Oberholser 1938, Oberholser and Kincaid 1974, Wayne 1910), although colonies outside Florida formed irregularly and contained few birds. The United States population of storks was not greatly disturbed during the plume-hunting era (Allen 1958), and probably contained between 75,000 and 100,000 birds of all age classes during the early twentieth century (Ogden 1978). Increased land development and the associated drainage of freshwater wetlands eliminated many nesting and feeding sites, resulting in a severe decline in the total number of storks. Concern for the fate of this species in the United States was first expressed during the late 1950s (Allen 1958, Sprunt and Kahl 1960).

A series of aerial surveys was conducted between 1957 and 1960, in an attempt to locate all remaining Wood Stork nesting colonies in the United States. Renewed concern for the status of storks during the early 1970s resulted in a second series of aerial surveys beginning in 1974. These 2 surveys produced the first complete counts of the number of storks nesting in the United States, and revealed that major colonies continued to decline between surveys. In this paper we present the results of the aerial surveys and discuss probable reasons for the Wood Stork decline to call attention to the seriously threatened status of this species in the United States.

METHODS

One or more aerial surveys were made during breeding seasons over all of peninsular Florida annually between 1957 and 1960, and again between 1974 and 1976. The surveys checked all known or suspected stork nesting colonies and systematically searched for unknown colonies in regions where habitat appeared suitable or where numbers of feeding storks were known. Wood Storks construct large nest platforms in the upper layers of woody vegetation, thus nests are conspicuous from the air. Although we believe that aerial estimates of pairs in colonies are accurate, verification was attempted at most colonies during both series of surveys by ground counts of nests. Aerial surveys and verification during 1957–1960 were conducted by Alexander Sprunt, IV and M. Philip Kahl of the National Audubon Society, and John Storer and Lisa Von Borowsky of the Florida Audubon Society. The 1974–1976 surveys of central and southern Florida were conducted primarily by Ogden, while the northern Florida and Georgia colonies were checked by Nesbitt.

TABLE 1
PAIRS OF NESTING WOOD STORKS IN UNITED STATES COLONIES, 1959–1960, AND 1975–1976

Colony	1959	1960	Colony	1975	1976
Guano Lake	50	50	Craven Hammock	0	16
River Styx[1]	450	150	River Styx	100	70
Panasoffkee	125	120	Dee Dot	85	125
Croom	325	300	Croom	85	0
Lacoochee	0	40	Cabbage Swamp	?	45
Panther Point	40	120	Lake Yale	150	110
Tenoroc	120	10	Turnbull	100	50
Pelican Island	2	0	Pelican Island	275	160
Reedy Creek	215	200	Moore Creek	150	225
Charlie Creek	175	35	Little Gator Creek	(active)	150
Barley Barber	?	200	Mulberry	(active)	450
			Payne Creek	0	4
			Cypress Creek	75	40
			El Clair	0	250
Central-North totals	1502	1225		1020 (1620)[2]	1695
Corkscrew	4000	4700	Corkscrew	3000	2100
Sadie Cypress	5	1400	Sadie Cypress	27	40
Deep Lake	150	0	Lane River	1100	1200
Rocky Lake	0	235	Madeira	125	0
East River	1000	1500	East River	110	75
Cuthbert	1000	1000			
South-west totals	6155	8835		4362	3415
Totals	7657	10,060		5382 (5982)[2]	5110

[1] Also known as Micanopy.
[2] Adjusted total derived from 1976 counts.

RESULTS AND DISCUSSION

Kahl (1964) identified 3 regions of Florida where Wood Storks nest, the Everglades-mangrove, Big Cypress, and Lake districts. Because of strong similarities in seasons of activity and recent population trends between the Everglades and Big Cypress districts, we have combined these 2 into a Southwest Florida region. Also, we have re-named Kahl's "Lake District" as the Central-North Florida region, to include all of Florida and southern Georgia north of Lake Okeechobee. We do not consider storks nesting within a region to represent a distinct subpopulation. Colonies in the Southwest Florida region usually form each year between November

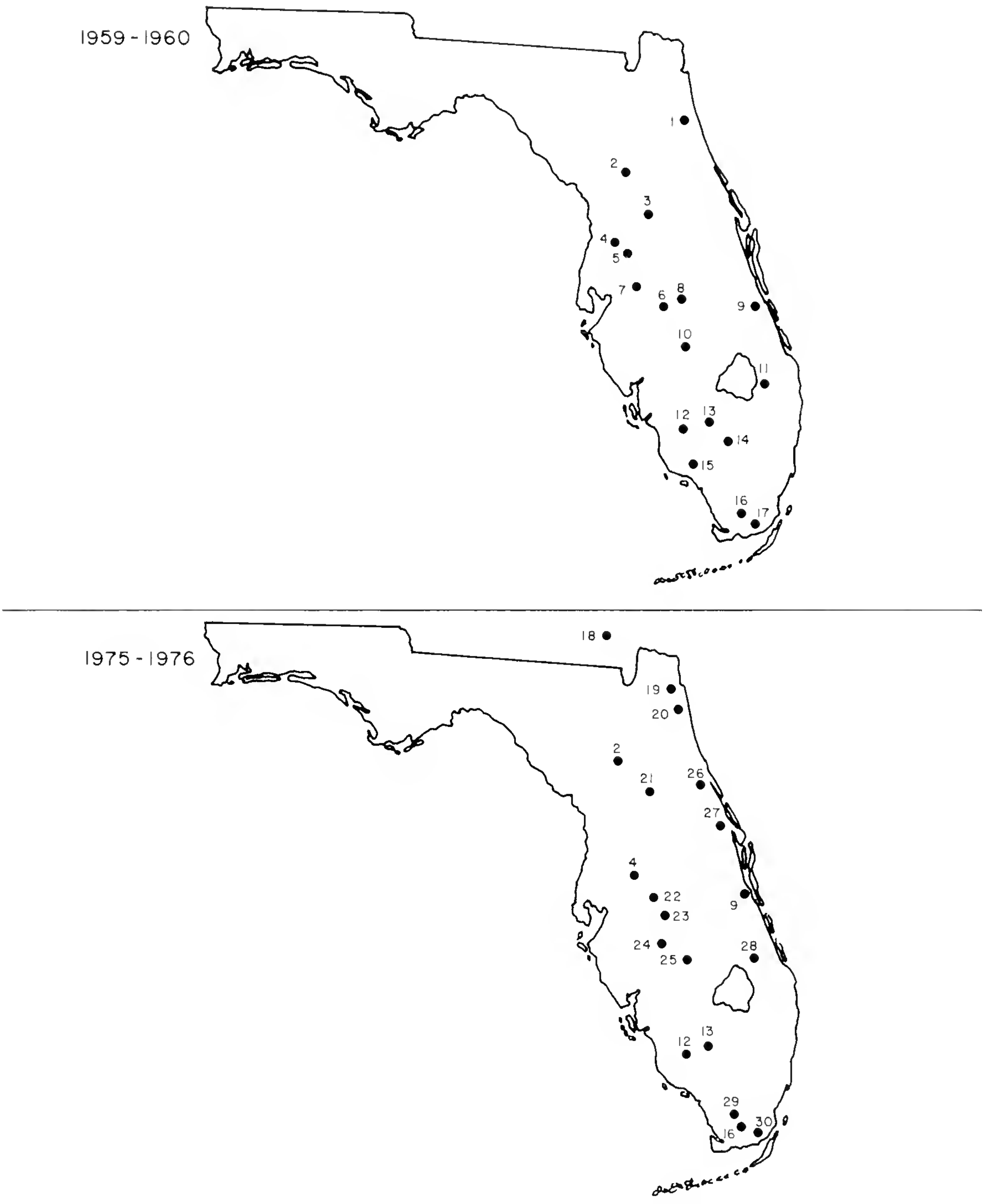

FIG. 1. Location of active Wood Stork colonies during 1959–1960 and 1975–1976 surveys. Numbered sites are as follows: (1) Guano Lake, (2) River Styx, (3) Panasoffkee, (4) Croom, (5) Lacoochee, (6) Panther Point, (7) Tenoroc, (8) Reedy Creek, (9) Pelican Island, (10) Charlie Creek, (11) Barley Barber Cypress, (12) Corkscrew, (13) Sadie Cypress, (14) Rocky Lake, (15) Deep Lake, (16) East River, (17) Cuthbert, (18) Craven Hammock, (19) Dee Dot Ranch, (20) Cabbage Swamp, (21) Lake Yale, (22) Little Gator Creek, (23) Mulberry, (24) Payne Creek, (25) El Clair, (26) Turnbull Slough, (27) Moore Creek, (28) Cypress Creek, (29) Lane River, (30) Madeira.

and January, while Central-North Florida colonies form between February and April. In both regions, colony formation occurs during annual dry seasons, when water levels normally drop and food resources are concentrated (Kahl 1964, Kushlan et al. 1975).

The numbers of breeding pairs of Wood Storks in the United States population during the 2 series of surveys are presented in Table 1. Locations of active colonies are shown in Fig. 1. Counts made during the last 2 years of each survey period were the most accurate because of the cumulative improvement in technique and knowledge of nesting localities; only these data are used in this report. The colonies at Mulberry and Little Gator Creek were active in 1975 but not surveyed. Assuming that the 2 sites contained approximately the same numbers in 1975 as in 1976, as suggested by reports of local observers, we parenthetically included an adjusted 1975 total which we believe is more accurate. Results of the 1974 survey, and of partial surveys in 1972 and 1973, were presented by Ogden (1972, 1973, 1974) and Nesbitt (1973).

Table 1 shows that the overall number of breeding storks in the United States declined 41% in the 15 years between the high counts of 1960 and 1975. On a regional basis, the 2 year mean in the Central-North region increased between the 2 series of surveys by 17% (1363 to 1657 pairs), while the 2 year mean in Southwest Florida declined 48% (7495 to 3888 pairs).

We found the number of pairs nesting in all colonies within a region was greater during some years than others, implying that inter-region feeding conditions and weather are more favorable in some years than others and that not all adult storks attempt nesting in the poorer years. To determine the total number of breeding pairs of storks in the population during each of the surveys, therefore, requires that each survey period contain a favorable year when most adults are in colonies and can be counted. The annual climatological pattern that appeared to stimulate the heaviest nesting efforts by storks was a combination of average or above-average rainfall during the summer rainy season prior to colony formation, and an absence of unusually rainy or cold weather during the following winter–spring nesting season. This pattern produced widespread and prolonged flooding of summer marshes that maximized production of freshwater fishes, followed by steady drying that concentrated fish during the dry season when storks nest (Kahl 1964). Recent studies in south Florida show that since the 1960s the Everglades and Big Cypress ecosystems have produced large numbers of young storks only in years with exceptionally dry winter and spring seasons (Kushlan et al. 1975, Browder 1976).

Pertinent rainfall data for the 1959, 1960, 1975 and 1976 nesting seasons are presented in Table 2. These data show an acceptable wet summer–

TABLE 2
SEASONAL RAINFALL PATTERNS AT 7 FLORIDA STATIONS[1]

Station	Prior to 1959 nesting		Prior to 1960 nesting		Prior to 1975 nesting		Prior to 1976 nesting	
	June–Oct. 1958 rainy season	Nov.–Feb. 1958–59 dry season	May–Oct. 1959 rainy season	Nov.–Feb. 1959–60 dry season	June–Oct. 1974 rainy season	Nov.–Feb. 1974–75 dry season	May–Oct. 1975 rainy season	Nov.–Feb. 1975–76 dry season
Jacksonville	−9.74	+5.91	−7.69	+1.00	+5.38	−5.12	−3.43	−5.22
Gainesville	−3.87	+4.38	+1.98	−1.52	+3.71	−2.23	+0.33	−3.91
Orlando	−7.40	+4.99	+3.98	+1.90	+4.30	−6.42	+4.60	−6.32
Lakeland	−11.63	+3.17	+2.71	−0.07	+5.28	−5.66	−2.61	−3.61
Ft. Pierce	−8.34	−0.86	+13.11	+3.81	+4.71	−6.75	−5.78	−2.73
Ft. Myers	−2.60	+2.03	+8.93	+1.80	+12.36	−5.82	+5.14	−3.69
Miami	−6.23	+6.70	+21.43	+8.74	−5.99	−0.38	−13.24	−0.73
Mean deviation	−7.11	+3.76	+6.35	+2.23	+4.25	−4.62	−2.14	−3.74

[1] Expressed as the cumulative of monthly deviations above (+) or below (−) average rainfall, in inches; data from National Oceanic and Atmospheric Administration.

dry winter pattern of rainfall before and during the 1960 nesting season, and an especially favorable wet–dry rainfall pattern during the 1975 nesting season. We assume that counts of nesting storks during these 2 seasons should include most of the adult birds in the 2 regions. For the south Florida colonies, which have been monitored most consistently, it is known that the number of storks that attempted to nest in 1975 in the Southwest Florida region was greater than during other years of the 1970s (J. Hansen, J. Ogden, pers. obs.).

The kinds of sites used by nesting storks are shown in Table 3. Each colony is categorized by the dominant vegetation where nests were located, whether the colony used a natural site or one altered by past human activity, and whether the site appeared secure from harmful intrusion by humans. We considered a colony to be secure if the land owner was aware of the colony, if human intrusion into the colony was controlled, and the colony site did not appear subject to future physical change due to an action of the owner.

All active colonies seen during the 1974–1976 surveys were in trees over standing water, or on islands. Thus the kind of altered sites acceptable to nesting storks were mainly artificial water impoundments where large trees were left standing. All altered sites were in the Central-North Florida region. Two altered sites contained approximately 10% of the pairs in the Central-North Florida region in 1959 and 1960, 4 altered sites contained 46% of the region's storks in 1975, and 6 altered sites contained 59% in

TABLE 3

GENERAL CHARACTERISTICS OF WOOD STORK NESTING COLONIES

	Location	Dominant vegetation	Natural or altered site	Status-ownership
1959–1960 colonies	Guano Lake	Cypress	Natural	Secure-private
	Panasoffkee	Cypress	Natural	Insecure-private
	Lacoochee	Cypress	Natural	Insecure-private
	Tenoroc	Dead Cypress	Water impoundment	Secure-private[1]
	Panther Point	Dead hardwoods	Water impoundment	Secure-private[1]
	Reedy Creek	Cypress	Natural	Insecure-private
	Charlie Creek	Cypress	Natural	Insecure-private
	Barley Barber	Cypress	Natural	Insecure-private
	Deep Lake	Cypress	Natural	Secure-private
	Rocky Lake	Cypress	Natural	Insecure
	Cuthbert	Mangrove	Natural	Secure-Federal
Active both years	River Styx	Cypress	Natural	Insecure-private
	Croom	Cypress	Natural	Insecure-private
	Pelican Island	Mangrove	Natural	Secure-Federal
	Corkscrew	Cypress	Natural	Secure-Audubon
	Sadie Cypress	Cypress	Natural	Insecure-private
	East River	Mangrove	Natural	Secure-Federal
1975–1976 colonies	Craven Hammock	Cypress	Natural	Secure-Federal
	Dee Dot	Cypress	Water impoundment	Secure-private
	Cabbage Swamp	Cypress	Natural	Insecure-private
	Lake Yale	Cypress	Natural	Insecure-private
	Turnbull	Cypress	Natural	Insecure-private
	Moore Creek	Mangrove	Natural	Secure-Federal
	Little Gator Creek	Cypress	Backwater pumping	Insecure-private
	Mulberry	Dead hardwoods	Water impoundment	Insecure-private
	Payne Creek	Dead hardwoods	Water impoundment	Insecure-private
	El Clair	Cypress	Water impoundment	Secure-private
	Cypress Creek	Cypress	Water impoundment	Insecure-private
	Madeira	Mangrove	Natural	Secure-Federal
	Lane River	Mangrove	Natural	Secure-Federal

[1] Became Florida Audubon Society sanctuaries in December 1959.

1976. The percentage of storks nesting at secure sites was 72% in 1960 and 80% in 1975.

Before action can be taken to stabilize the remaining Wood Stork population, it is necessary to understand the causes for the recent decline. Population stability is dependent upon maintenance of suitable nesting sites, and on the extent and productivity of wetland feeding sites. We know of no other factors that have had an important role in the recent dynamics of storks in Florida. No pesticides or other environmental pollutants have been shown to have affected reproduction rates or total numbers of fish-eating birds in Florida (Blus et al. 1974, Ogden et al. 1974). Shooting of storks is rare. Most storks remain in Florida during non-breeding seasons, although hundreds disperse northward in some summers, primarily into coastal Georgia and South Carolina (Ogden, pers. obs.). No major habitat changes or other factors that would adversely affect large numbers of non-breeding storks in these 3 states are known to us. We therefore consider that the stork decline has been caused by one or more of the following factors: (1) reduction in the number of available nesting sites, (2) lack of protection at nesting sites, and/or (3) loss of an adequate food base during the nesting season.

Data in this paper show no positive correlation between numbers of colony sites and stability of regional nesting groups of Wood Storks. Statewide, the number of colonies was nearly the same during the 2 series of surveys: 17 in 1959–1960 and 19 in 1975–1976. In Southwest Florida, where stork numbers have declined sharply, the number of nesting sites has dropped only from 6 to 5. The drop in number of colonies, however, is unrelated to loss of nesting sites. The small colonies at Deep Lake and Rocky Lake likely were satellite colonies of Corkscrew, and although unchanged, have been abandoned only because the number of storks using Corkscrew has dwindled. Stork nesting at Madeira began the year after a major 1960 hurricane killed many trees at the nearby Cuthbert colony, although vegetation at the latter site has since recovered. In Central-North Florida, neither the geographical distribution nor total number of colonies greatly changed between the 2 series of surveys. Considerable shifting about by storks did occur, however, with only 3 of 11 sites active during both surveys. The fact that the percentage of birds nesting in impoundments and on mangrove islands dramatically increased suggests that although storks in this region may not yet be short of nesting sites, undisturbed cypress swamps that traditionally have been favored habitat are now in short supply.

Our impression of why cypress swamps in central Florida are now less frequently used by storks is based on observation and speculation. Lowered surface water levels due to drainage and numerous water management schemes have resulted in cypress swamps being dry more often in recent years than earlier, during the natural spring dry season when stork colonies form. Since storks in Florida characteristically nest in woody vegetation over water, or on islands surrounded by open water, fewer suitable cypress nesting sites have been available in recent years due to the dryness. During our surveys each year prior to the summer rainy season, we have seen many dry cypress swamps that appeared otherwise suitable for nesting storks, including former or occasional colony sites at Croom, Lacoochee, Reedy Creek, Charlie Creek and Barley Barber Cypress.

The second suggested cause of the stork's decline, lack of protection from human disturbance at existing colonies, is not supported when colony histories are compared with colony protection. The largest Florida stork colonies at Corkscrew and in Everglades National Park have been among the best protected; these are the major colonies in the Southwest Florida region where storks have shown dramatic decline.

No clear relationship between colony security and population trends is evident in the Central-North Florida region. Two of the 3 colonies active during both series of surveys were insecure sites, while the 8 colonies that became inactive between surveys included 3 secure and 5 insecure sites. Two of the inactive, secure colonies were in surface phosphate impoundments (Tenoroc and Panther Point), and were lost due to shifting mining operations (that also create new colony impoundments). The 5 inactive, insecure colonies were all in natural cypress swamps and probably were abandoned because they became too dry, as described above, rather than because of human disturbance.

The third suggested factor, that storks have declined due to loss of an adequate food base, is supported by strong circumstantial evidence. Wood Storks feed primarily in freshwater sites, and use a grope-feeding technique that requires both high densities of fish and certain sizes of fish (Kahl 1964, Ogden et al. 1976). Storks also are larger than other Florida ciconiiforms and have higher food requirements in order to achieve successful nesting (shown in comparison to the White Ibis [*Eudocimus albus*] by Kushlan 1977). Therefore, any reduction in the food base or availability of fish in Florida wetlands will adversely affect storks sooner or more severely than other waders. Unfortunately, quantitative data on freshwater fish numbers in Florida wetlands prior to the 1960s are lacking, so we cannot demonstrate long-term quantitative changes in fish numbers or availability in Florida's freshwater ecosystems. Related studies and observations (cited below), however, strongly suggest that storks have become stressed by food shortages, both due to loss of feeding habitat and to adverse changes in fish biomass or availability in remaining wetlands.

Assuming fish numbers are dependent upon area of wetland habitats, then important food resources have been reduced, at least in south Florida, because a considerable portion of the freshwater wetland habitats have been eliminated during the twentieth century. Browder et al. (1976) categorized different wetland types south from the Lake Okeechobee system, and showed change in distribution and total acreage of each between 1900 and 1973. We combined 5 of these categories of freshwater habitats that

TABLE 4

NESTING SUCCESS AT WOOD STORK COLONIES WITH KNOWN OUTCOMES, 1971–1976[1]

Colony location	1971	1972	1973	1974	1975	1976
Central-North region						
Craven Hammock						F
Black Hammock			S			
Dee Dot	S	S	S	S	S	S
Cabbage Swamp						S
River Styx	S				F	
Lake Yale				S	S	
Turnbull						F
Moore Creek			S	F	S	S
Grant			S			
Pelican Island	S	S	S	S	S	S
Croom	F				S	
Reedy Creek	F					
Mulberry						S
El Clair	S		S	F		S
St. Johns Drainage	F			F		
Barley Barber	S	S		F		
Southwest region						
Corkscrew	S	F	F	S	S	S
Lane River			F	S	S	F
East River	F	F	F	S	S	F
Cuthbert	F	F	F			
Madeira	F	F	F	S	F	F

[1] S = success, F = failure.

are most important as feeding sites for storks (cypress domes and strands, wet prairies, scrub cypress, freshwater marshes and sloughs, and sawgrass marshes), and determined that the acreage of these 5 has been reduced by 35% since 1900. Thus, storks feeding in south Florida lack the number of feeding site options they once had.

Perhaps a more serious problem for storks than loss of feeding habitats are changes that must have occurred in remaining wetlands. Tracts of freshwater marshes and swamps remain throughout peninsular Florida, which on the basis of area alone appear to be capable of supporting greater numbers of storks than at present. Most are either impounded, partially drained or otherwise altered, and we suggest that these managed wetlands fail to maintain an adequate food base for Wood Storks, either by not producing enough fish or by not concentrating the fish in proper depths of water at the proper season. Supporting field data for this contention is at best tenuous. Allen (1958) discussed the effects of reduced production of fish in an altered wetland, related to declining wading bird populations, when he reported his impressions of reduced fish abundance in the Everglades between the 1930s and 1950s. Ogden (1978) summarized recent population trends by colonial ciconiiforms on the Atlantic and Gulf coastal plains, and showed that most species or populations have been stable or increasing since the 1950s, except in some freshwater regions. The most serious declines occurred in the interior of Florida and involved several species with diverse food habits and feeding techniques, such as Snowy Egrets (*Egretta thula*), Little Blue Herons (*Hydranassa caerulea*), White Ibis and Wood Storks. Our assumption is that most remaining freshwater habitats have become less productive, a trend that adversely affects both density and biomass of a broad range of wading bird prey species.

Our subjective observations support the conclusion that altered freshwater wetlands in Florida are less productive, at least for the sizes of fish taken by storks. In the Everglades, storks no longer feed at peripheral wetland sites where they once were frequently reported (E. Winte, C. Brookfield, pers. comm.), a clue that shortened hydroperiods in this heavily managed system have adversely altered fish production or growth rates.

Stork nesting in the Central-North region apparently remained stable between 1960 and 1976 because of a higher frequency of nesting success in these colonies than in south Florida. Thirty-eight monitored nesting attempts at 16 different Central-North colonies between 1971 and 1976 (Table 4) resulted in 28 successful nestings (74%). We defined a successful nesting as one in which the number of fledged young equalled or exceeded the number of pairs of adults in the colony. In the Southwest Florida region, 25 nesting attempts at 5 colonies between 1971 and 1976 resulted in only 9 successful nestings (36%: pers. obs., J. Hansen, W. Robertson, J. Ogden).

Data on distribution and abundance of stork food are not sufficient to explain the higher rate of colony success in the Central-North region. It is interesting, however, that all south Florida colonies failed in 2 of the 6 years between 1971 and 1976, whereas some Central-North colonies were successful each year. The south Florida colonies are more geographically clumped and often show similar rainfall and water level patterns, and it is not surprising that adverse nesting conditions influence all colonies during the same year. The Central-North Florida region is geographically larger, and stork colonies are associated with many, widely separated wetland systems. The probability that conditions for successful nesting would be lacking throughout this region during any year is apparently low. So it appears that stability in the Central-North region is at least in part due to the geographical spread in colonies.

SUMMARY

Surveys of the resident population of Wood Storks in the southwestern United States showed that numbers of breeding adults declined 41% between 1960 and 1975. The decline has been sharp in the large south Florida colonies, while the number of birds breeding in a scatter of smaller colonies between central Florida and southeastern Georgia has remained stable or slightly increased. Reasons for the decline are discussed, including loss of colony sites, lack of protection at colonies, and loss of an adequate food base. We conclude, largely through circumstantial evidence, that the single important factor responsible for the stork decline has been a loss of feeding habitats coupled with a reduction in fish biomass or food availability in remaining wetlands.

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DISPLAYS AND MORPHOLOGY OF AN ANNA × ALLEN HUMMINGBIRD HYBRID

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Hybrids between the Anna (*Calypte anna*) and Allen (*Selasphorus sasin*) hummingbirds have been reported by a number of authors (Williamson 1957, Banks and Johnson 1961). Displays and vocalizations of such hybrids have hitherto not been described. Moreover, all hybrids discovered so far have presumably involved the migratory *S. s. sasin* as one of the parents. We report here the first record of a hybrid between *C. anna* and the non-migratory *S. s. sedentarius*, describe its displays and vocalizations, and discuss the ecological circumstances which may have permitted hybridization between the 2 parental forms.

HISTORY OF THE HYBRID

The hybrid was first observed on 9 March 1976, in the South Coast Botanic Garden, Palos Verdes Peninsula, Los Angeles Co., California (map in Wells, Bradley and Baptista 1978). It was observed chasing a number of Allen Hummingbird males that held adjacent territories.

The hybrid was netted on the evening of 15 March and ringed with a U.S. Fish and Wildlife Service aluminum band. At that time, kodachromes of all diagnostic features, notes, measurements and weight were taken. A few feathers showing diagnostic features were removed for preservation from the gorget, including longest right and left "gorget tails," from among the longest undertail coverts, and from the upper tail coverts, breast and vent. These have been deposited in the Moore Laboratory of Zoology (ML66272). We did not remove the outermost rectrix, a most important diagnostic feature, so as not to impede in any way the displays of the hybrid. However, shape and color of the rectrices are shown very clearly on our color prints (H2 in Fig. 1).

The hybrid was released at 10:55 on 16 March. Its territory meanwhile had been taken over by an Allen Hummingbird. The hybrid subsequently moved to another part of the garden where it was located on 2 April and was studied periodically until 21 April.

DESCRIPTION OF HYBRID

This description is based on detailed notes, made when the hybrid was in hand, aided by kodachromes showing all the diagnostic features. Color of gorget also is based on a few feathers from the hybrid and compared with museum specimens of the parental forms. Specimens of the latter were taken from March to December and, therefore, included at least some specimens in comparable state of feather wear with the hybrid.

Capital tract.—Gorget color of *C. anna* is metallic rose red, changing to solferino and violet in certain lights (Ridgway 1911:619). Gorget color

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[1] Deceased.

in *S. sasin* is more orange (coppery) red. Gorget color in the hybrid was intermediate, tending toward *anna.* Feathers at the base of the hybrid's bill were rufous, a few with green centers. This last feature was also found in Williamson's (1957) hybrid.

Iridescent gorget feathers are confined to the throat in *S. sasin,* but extend over the forehead and crown in *C. anna.* Gorget shape in the hybrid was similar to *C. anna.* However, the iridescent purple feathers in the hybrid did not extend as far back over the head as in *anna.* In the hybrid, feathers in the loral, superciliary and auricular regions were tinged with rufous, characteristics of *sasin.* This was similar to hybrid B of Banks and Johnson (1961). The white postocular stripe of both parental forms was also present in the hybrid.

Spinal tract.—The nape, back and rump are metallic green in *anna.* In *sasin,* the nape and back are rufous-tipped and the rump is entirely rufous. The hybrid was green throughout, except for slight hints of rufous tipping the rump feathers.

Ventral tract.—Gorget "tails" are 12–13 mm in both parental forms. The right gorget tail measured 12.8 mm in the hybrid. The iridescent portion on the gorget tail in *anna* measures approximately 5 mm ($N = 22$). The latter is 4 mm in *sasin* ($N = 13$) and 5 mm in the hybrid. The basal portion of the iridescent gorget feathers in *anna* is uniformly gray. These feathers have a broad (2.5–3 mm) band of rufous bordering green-gray in *sasin.* In the hybrid the rufous band was narrower than in *sasin* and was gray basally.

Feathers immediately below the gorget in the hybrid were whitish, reminiscent of *sasin.* In *anna* these feathers are grayer. In the hybrid, feathers of the sides and flanks were metallic green with tinges of rufous, the latter a character of *sasin.*

Alar tract.—The leading edge of the wing was rufous in the hybrid. Underwing coverts were green, some feathers edged with rufous. There was a large rufous patch in the axilars. The rufous areas are all *sasin* characters.

Caudal tract.—Dorsally, rectrix 1 is metallic green in *anna.* Rectrix 2 is less metallic and edged with gray in inner and outer webs. The latter may be buffy in a few specimens as noted earlier by Williamson (1957). All other rectrices in *anna* are black with grayish edges. All rectrices in *sasin* are rufous with various amounts of black on the distal tips and outer edges. Rectrices of the hybrid were similar in color and shape to those illustrated in Banks and Johnson (1961) and were intermediate in shape between the parental species. Rectrix 1 in our hybrid differed slightly in coloration from Banks and Johnson's (1961) specimen in that the green extended farther down the shaft in our bird (compare H1 and H2, Fig. 1).

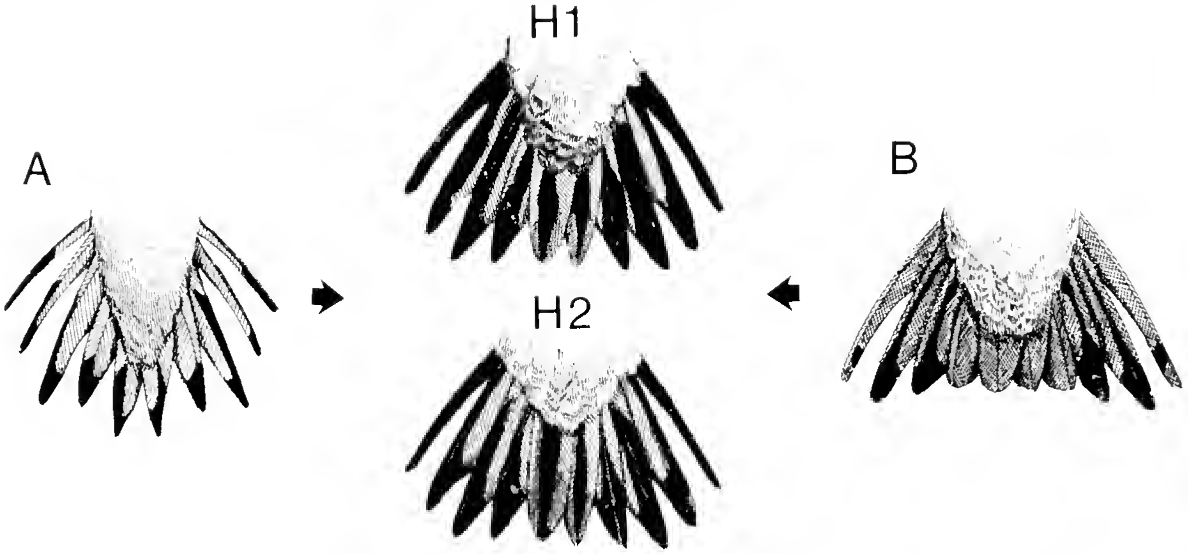

FIG. 1. Tails of (A) *Selasphorus sasin*. (B) *Calypte anna*. (H1) Hybrid *Calypte anna* × *Selasphorus sasin* from Banks and Johnson (1961). (H2) Hybrid *Calypte anna* × *Selasphorus sasin sedentarius* from this study drawn from kodachromes. Note more green (cross-hatching) on rectrix 1, and more rufous on rectrix 4 (diagonal lines) in our hybrid compared to Banks and Johnson (1961).

Undertail coverts in *sasin* are rufous but green or greenish-brown in *anna*. Undertail coverts in the hybrid were green edged with rufous. The longest pair of undertail coverts was black-tipped in Banks and Johnson's (1961) specimen, light green-tipped in our hybrid.

Measurements of the hybrid.—There is overlap between *S. sasin* and *C. anna* in all measurements. However, if only means are considered, the hybrid is intermediate in wing length and weight between *S. s. sedentarius* and *C. anna* (Table 1). Bill length of our hybrid is longer than means for either alleged parental type. It falls within the range of *sedentarius* and *anna*, but beyond that for nominate *sasin*.

EPIGAMIC DISPLAYS

Dive Displays

C. anna.—The dive display of the Anna Hummingbird has been described by a number of authors (review in Wells, Bradley and Baptista 1978). Briefly, the male flies upward 75–150 ft (22.8–45.5 m) above the female with his bill pointed down, sometimes pausing there to sing, then he flies still higher. At the top of his climb he pauses a second time, looking down at the female, often singing once more. He then dives over the female making a sharp *peek* (terminology after Cogswell 1957) (Figs. 2A and 4C) at the bottom of the dive. Thereafter, he may repeat the display, fly after the female, or fly to a perch and sing.

S. sasin.—The following description is from Bassett (1921) and Banks

Table 1

Measurements of Hybrid Anna × Allen Hummingbird and Males of the Parental Types

	N	Culmen	Wing	Weight
Selasphorus s. sasin[1]	20	14.1–16.3 (15.5 ± 0.13)	36.8–38.8 (37.9 ± 0.13)	2.8–3.9 (3.3 ± 0.11)[2]
Selasphorus s. sedentarius[3]	13	17.0–18.8 (17.62 ± 0.58)[b]	38.0–39.5 (38.73 ± 0.49)[b]	3.2–3.81 (3.52 ± 0.24)[a]
Calypte anna[1]	20	16.1–18.4 (17.4 ± 0.14)	47.8–51.2 (49.1 ± 0.19)	3.3–5.8 (4.3 ± 0.17)[4]
Hybrid 5[3]	1	18.6[5]	43.5	3.85

Values in brackets are means ± 1 standard deviation.

[a] One-tailed t-test, $P < 0.005$ when compared with nominate subspecies.

[b] One-tailed t-test, $P < 0.0005$ when compared with nominate subspecies. (One-tailed t-tests were used to demonstrate that Palos Verdes birds were larger than the nominate.)

[1] Data from Banks and Johnson (1961).

[2] 11 specimens.

[3] Data from this study, material from Palos Verdes, California, the *sedentarius* data are from live specimens subsequently banded and released.

[4] 10 specimens.

[5] Note that this value is much larger than the range for the nominate form, indicating *sedentarius* as one of the parental forms.

and Johnson (1961) supplemented with our notes. The male *sasin* flies back and forth over the female, tracing arcs 20 to 30 ft (6.1–9.1 m) across. At the end of each arc (points b and c in Fig. 2B) the male spreads his tail and shakes violently, making a high pitched (7.5 to 12 kHz) chirruping sound (Fig. 3A), lasting about 0.8 sec. After a number of these horizontal arcs, he flies upward 75 to 100 ft (22.8–45.5 m). During the climb his bill is pointed upward and his flight is slow and heavy, "describing spirals or undulations until he reaches the top" (Bassett 1921:37). Without pausing at the zenith, he then dives. Pearson (1960) has computed the speed of flight at various parts of the dive as varying from 34 to 64 mph (54.4–102.4 kmph). At the bottom of his dive he makes a mechanical ripping sound, *tup tup tup trrrr*! On the audiospectrograph this appears as an interrupted whistle at about 1.75 kHz with overtones at 3.5 and 5.25 kHz (Fig. 4A). The entire display may be repeated a number of times, or he may fly after the female. This display also is used against intruders. The displayer sometimes changes the direction of his horizontal arcs in the middle of his display (Baptista, pers. obs.).

C. anna × *S. sasin*.—The hybrid flew upward some 50 ft (15 m). During ascent his bill was pointed down as in *anna* but he traced an undulatory path similar to *sasin*. The bird sometimes paused at the zenith with bill pointing downward for 3–8 sec as in *anna*, or dived immediately as in

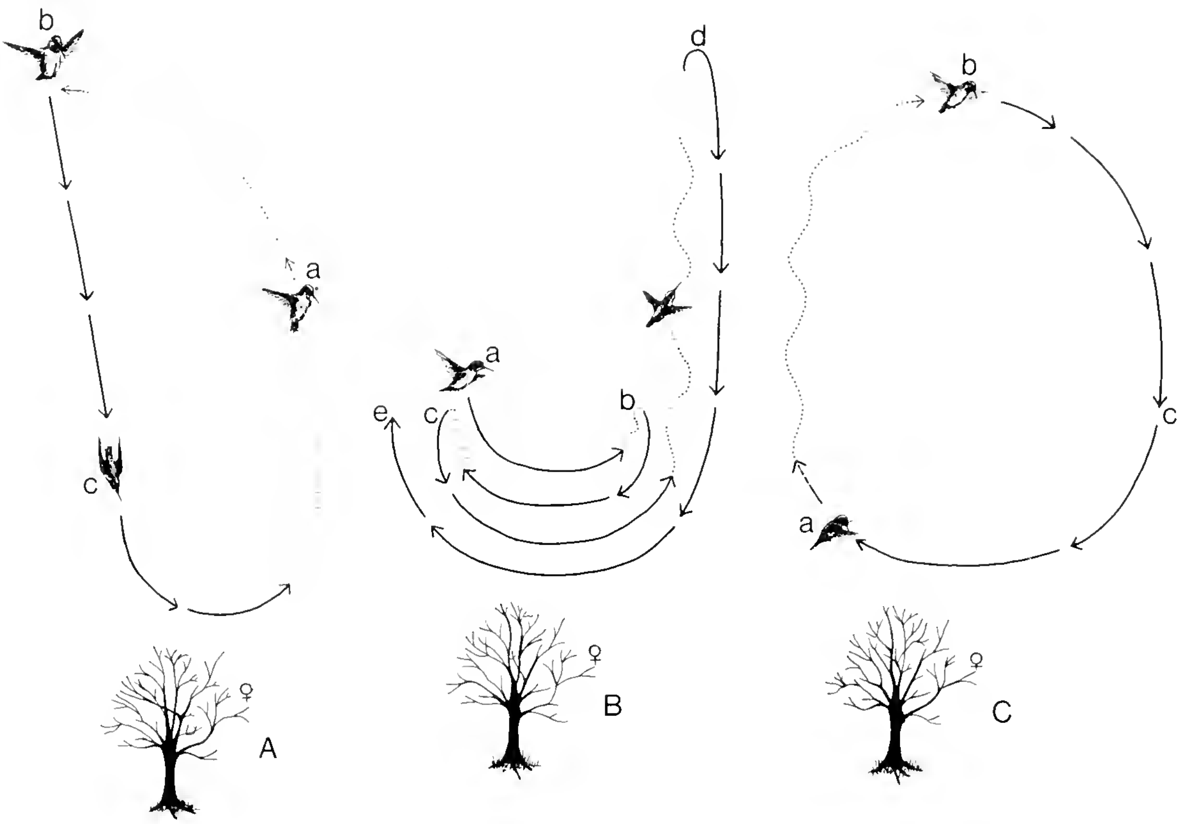

FIG. 2. (A) Display of *Calypte anna*, modified from Wells, Bradley and Baptista (1978). (B) Display of *Selasphorus sasin*, modified from Bassett (1921). (C) Display of Anna × Allen hybrid.

sasin. The arc at the top of the climb is much rounder in the hybrid than in either parental type (Fig. 2C). At the bottom of the dive it made a "pop" sound.

The "pop" sound is very similar to *sasin* in morphology and spectral structure, with a fundamental interrupted whistle at 1.75 kHz and overtones at 2.75 and 4.75 kHz (Fig. 4B). Its temporal structure, however, is very similar to *anna*. At no time was it heard singing during a display dive.

Static Song

Static song is unknown in *S. sasin* (Pitelka 1942, pers. obs.). Static song of *C. anna* is loud and elaborate (spectrographs in Mirsky 1976, Wells et al. 1978, Fig. 3B this study) and may last over 3 sec. The hybrid Anna ×Allen sang its static song in a posture very similar to the Anna Hummingbird, i.e., with body sloped forward and head turning from side to side to flash the gorget. The structure of the hybrid's song (Fig. 3C, D), however, is quite unlike the Anna's and consists of 2 or 3 chip notes 3.5–5.5 kHz in frequency, each chip lasting about 0.02 sec. Each chip was separated from the next by intervals of 0.13–0.37 sec.

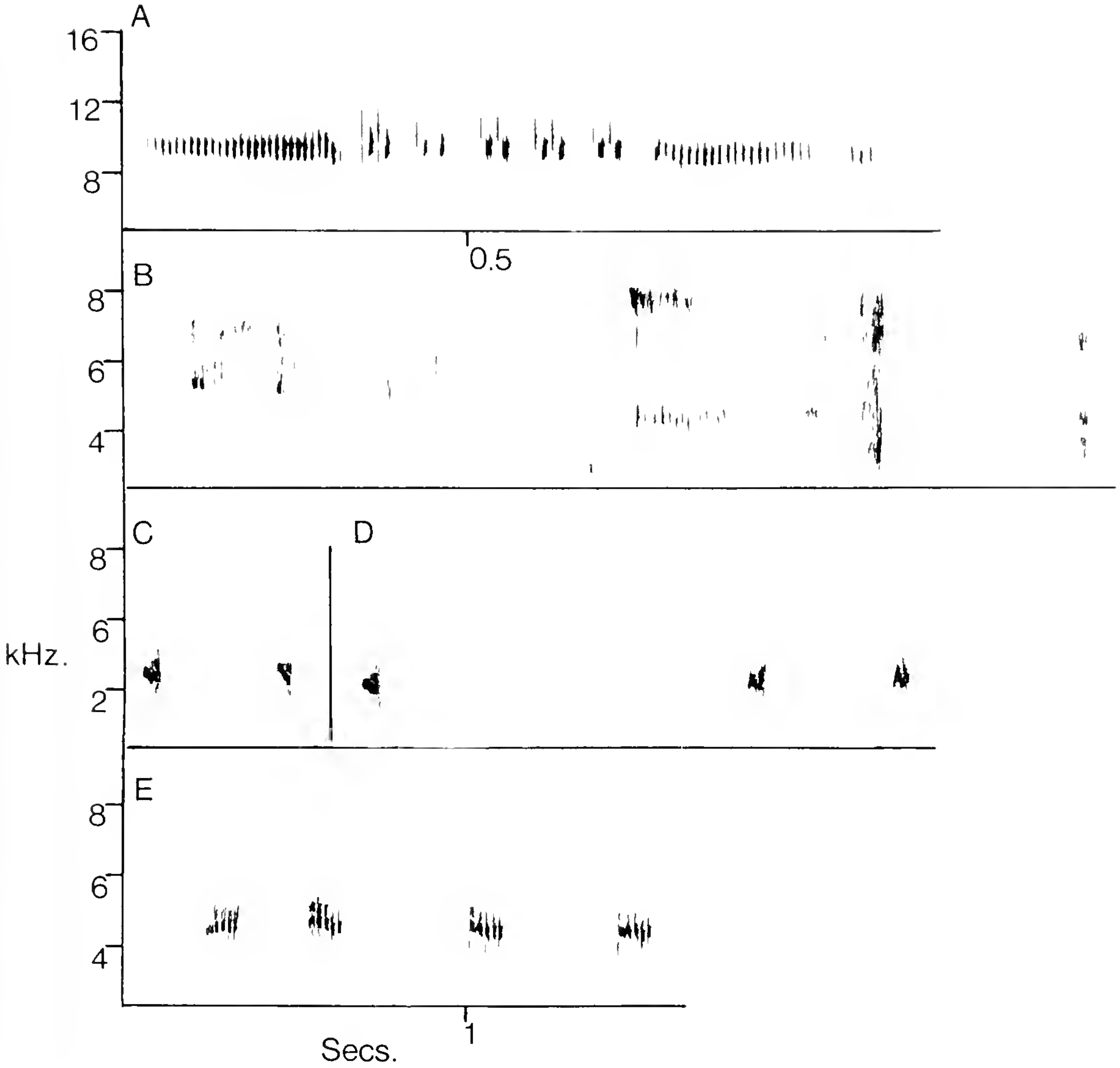

FIG. 3. (A) Twittering noises during pendulum display of *Selasphorus sasin*. (B) Portion of song of *Calypte anna*. (C), (D) Two songs from hybrid Anna × Allen. (E) Song of aberrant *Calypte anna* recorded on the Palos Verdes Peninsula, California on 9 December 1976 (see text).

An aberrant Anna Hummingbird song.—On 19 December 1976, we looked for the Anna × Allen hybrid and found an unbanded male Anna Hummingbird in full adult plumage occupying its territory. This bird sang a song unlike any Anna Hummingbird we have ever encountered (Fig. 3E) and unlike subsong of immature birds. The song was stereotyped and consisted of short trills, each trill being between 3.00–4.00 kHz in frequency and lasting about 0.04 sec. Trills were separated from each other by intervals of 0.07–0.13 sec. Since pitch and duration of trills were similar to pitch and duration of chips of the hybrid's song, we at first thought we were observing the hybrid. We soon learned to distinguish the different

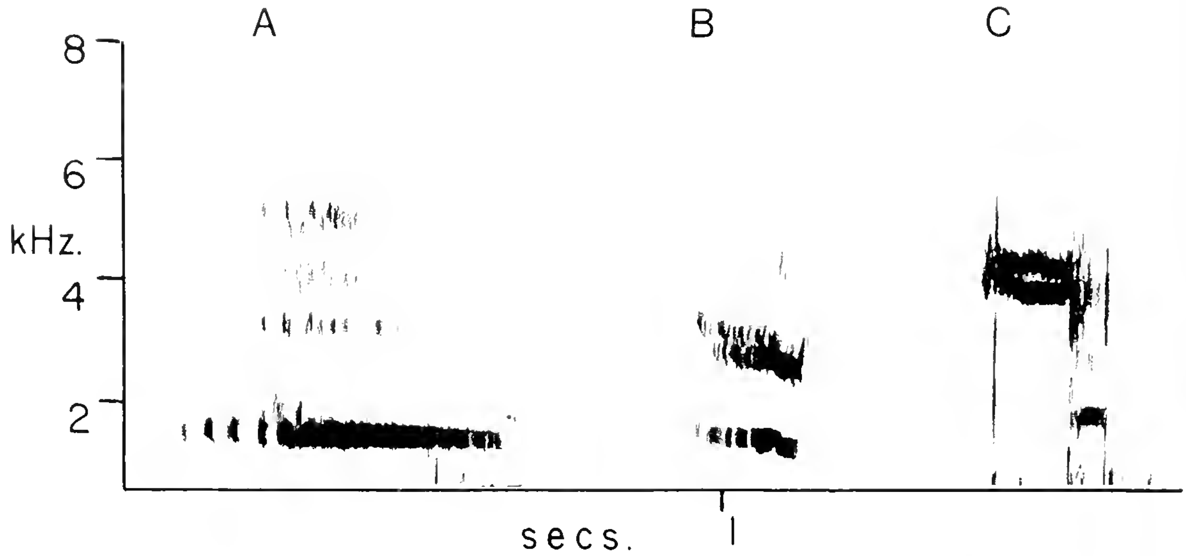

FIG. 4. (A) Sound at the bottom of the nuptial dive of *Selasphorus sasin*; (B) of Anna × Allen hybrid; (C) of *Calypte anna*. Note that the hybrid's sound resembles *Selasphorus sasin*'s in spectral structure, but *Calypte anna*'s in temporal structure.

tonal qualities in their respective songs. Unlike the hybrid, this Anna Hummingbird used its abnormal song in its aerial display.

Song in Anna Hummingbirds may be learned (Mirsky 1976). It is possible that this Anna Hummingbird displaced the hybrid from its territory and learned to produce a poor copy of the hybrid's song during male-male interaction. It is also possible that this apparently "pure" *anna* may have been a backcross to one of the parental forms. The hybrid was nowhere to be seen.

DISCUSSION

Breeding seasons of C. anna and S. sasin sedentarius.—*C. anna* and *S. s. sasin* breed sympatrically from Ventura County to the San Francisco Bay area of northern California (Grinnell and Miller 1944). On the Palos Verdes Peninsula, nests of *C. anna* have fresh eggs or nestlings from 22 December to 26 May (Wells, field notes). Allen Hummingbirds resident on the Palos Verdes Peninsula are referable to the subspecies *sedentarius* (Wells and Baptista, in press), and have been recorded nesting on the peninsula nearly year-round. There is, therefore, much overlap in the breeding season of *C. anna* and *S. s. sedentarius* at Palos Verdes, setting the stage for occasional interspecific hybridization. Wells made frequent observations of male Annas courting female Allens. The introduction of tropical flowering shrubs and trees on the peninsula may have induced Allen Hummingbirds to breed almost circumannually.

It is possible that our hybrid is the product of a mating between a *S. s.*

TABLE 2

FEATURES IN THE DISPLAY OF THE ANNA × ALLEN HYBRID COMPARED WITH THE ANNA AND ALLEN HUMMINGBIRDS

	Anna	Hybrid	Allen
Visual components			
Bill pointed down	+	+	–
Undulatory flight during climb	–	+	+
Pause high in air prior to climb	+	–	–
Pause at top of climb	+	±	–
Pendulum flight before climb	–	–	+
Acoustic components			
Static song display	+	+	–
Song in aerial display	+	–	–
Chirrup sounds during display	–	–	+
Dive sound an interrupted whistle	–	+	+
Dive sound short (±0.07 sec)	+	+	–
Fundamental of dive sound at 1.75 kHz	–	+	+

sasin and a resident *C. anna.* However, bill length of our hybrid is longer than previously reported hybrids and longer than the nominate *sasin*, a strong clue that *S. s. sedentarius* was one of the parents.

Display of the hybrid.—The displays of the hybrid were quite stereotyped in 10 of the 11 features studied (Table 2). The only variable character was the pause in the air at the top of the climb, an *anna* feature that was sometimes absent in the hybrid's display. We can recognize 6 *anna* characters and 5 *sasin* characters in the hybrid's displays (Table 2). The pendulum flight (Fig. 2), so characteristic of *S. sasin* displays, is absent in the hybrid. The structure of the hybrid's song (Fig. 3) resembles neither parent. It is noteworthy that the dive "pop" of the hybrid is similar to *S. sasin* in spectral structure, but more similar to *C. anna* in temporal structure (Fig. 4, Table 2). Hybrid displays contain components similar to both parental forms, intermediate between the 2 parental forms, or resemble neither parental form (review in McGrath et al. 1972, Baptista 1978). Our data indicate that the hybrid hummer's display contained elements from both parents. Its song resembled that of no hummingbird's described to date.

The display of the Anna × Allen hybrid resembles the display of the Anna × Costa Hummingbird (*Calypte costae*) hybrids (Wells et al. 1978) in that (1) the male ascends with head pointed down as in *anna*, and (2) song is absent in the aerial display.

SUMMARY

A hybrid between the Anna Hummingbird (*C. anna*) and Allen Hummingbird (*S. sasin sedentarius*) is described. The dive display of the hybrid shows components from both parental types. The hybrid's song resembles neither parent. Quasi-circumannual breeding has been found for both parental species on the Palos Verdes Peninsula, California, setting the stage for occasional hybridization.

ACKNOWLEDGMENTS

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SONG CHARACTERISTICS OF THE YELLOW WARBLER

Kenneth G. Bankwitz and William L. Thompson

The Yellow Warbler (*Dendroica petechia*) is one of the most widespread species of Parulidae; its breeding range extends from north-central Alaska to central Georgia, and from Newfoundland to northern Baja California (Bent 1953). In this paper we describe the general organization of Yellow Warbler song, variation in song form within a single individual and among different individuals, and some geographic variation in song characteristics.

METHODS

Bankwitz recorded the songs of 45 male Yellow Warblers in 2 widely separated areas of southern Michigan. The first of these was in Dearborn, a suburb of Detroit, in southeastern Michigan. A second, much larger area, included 6 different recording sites in Kalamazoo County, ca. 170 km west of Dearborn.

Recording techniques.—From 21 May through 2 June 1974, and on 28 May 1975, Bankwitz recorded with a Uher 4000 Report S tape recorder, an Electrovoice microphone, and a 50-cm aluminum parabolic reflector. From 19 June through 12 July 1974, and 6–10 July 1975, he used a Uher 4000 Report 1 C tape recorder. In 1974 and on 28 May 1975, recordings were made at 19 cm per sec; the remaining 1975 recordings were made at 9.5 cm per sec.

To facilitate accurate and complete notes, the date, time, weather conditions, location, and number of the male were spoken into the microphone before recording each individual. At least 20 songs of each territorial male were recorded whenever possible. Some individuals were recorded more than once during the day, between 04:00 and 21:00 EST, and on different days. One male was observed all day.

Because rain and strong winds tended to reduce the amount of singing, and because wind also distorted the recordings, recording was avoided during these conditions. Usually, undisturbed, territorial males were recorded. In a few instances Bankwitz recorded territorial disputes between males. He also recorded the response of males to the playback of tape recordings of their own or another male's song.

From a sample of 45 individuals, Bankwitz recorded 1328 songs of which 745 were analyzed using a Kay Electric Company Sona-Graph (model 661B) at the high shape and wide band settings. All song patterns from short song series were analyzed. When long sequences were composed of the same song pattern, as detected by ear, only a few songs from the beginning, middle, and end of the series were used. If the sequence contained different song patterns, each pattern distinguishable by ear was analyzed spectrographically. Song length and frequency range were measured on the sound spectrograms with the aid of a grid scratched on plexiglass. Song figures found in songs from southern Michigan were compared with figures from Yellow Warbler songs recorded in other parts of the United States and published on commercial phonograph records.

RESULTS

Analysis of song figures.—The smallest unit of the Yellow Warbler's song is the song figure. Shiovitz (1975) defines a song figure as "a sound

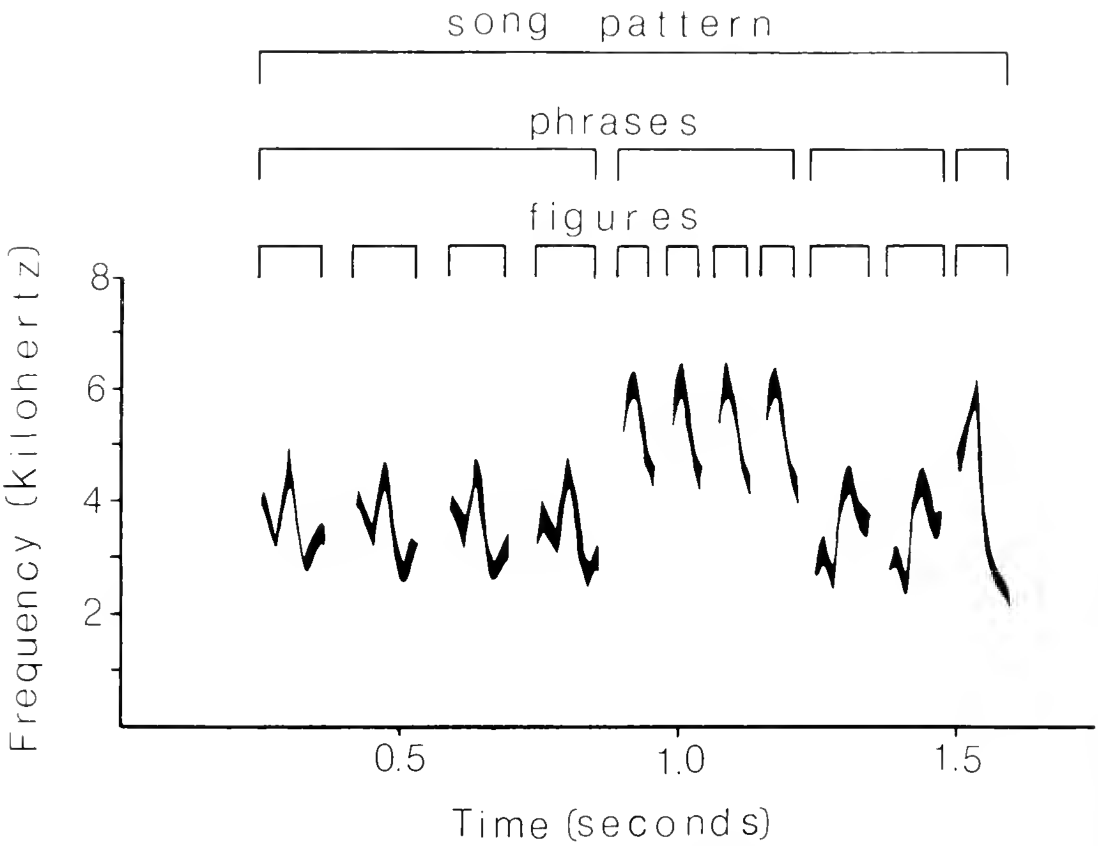

FIG. 1. Terminology applied to a typical Yellow Warbler song.

which produces a single, complete, and distinct impression uninterrupted by silences greater than two centiseconds." A song phrase is 1 or a series of identical figures comprising a group. Borror (1967) defined a "phrase" as a group of "notes" (=figures) repeated 1 or more times. A particular sequence of song phrases is a song pattern. All songs having the same arrangement and kinds of figures are said to have the same pattern. Fig. 1 illustrates the application of these terms to a spectrographic representation of a typical Yellow Warbler song.

Each different figure found in the songs was traced, transferred to drawing paper, and inked. These figures were then grouped according to frequency characteristics and similarity of shape to form a catalog (Fig. 2). From the 1974 and 1975 recordings we obtained 40 distinct figures.

Some figures occur only within 1 song pattern, while others are found in several. Similar figures are grouped in a song phrase within a given pattern. They vary slightly within a single song, and more in similar patterns sung by different individuals. However, the figures are sufficiently stable in form for us to designate them as the same. Some rather different figures, although clearly related, are connected within the population by a series of intermediates that grade almost imperceptibly from one extreme form to another. Fig. 3 shows variation in the form of figures sung by a

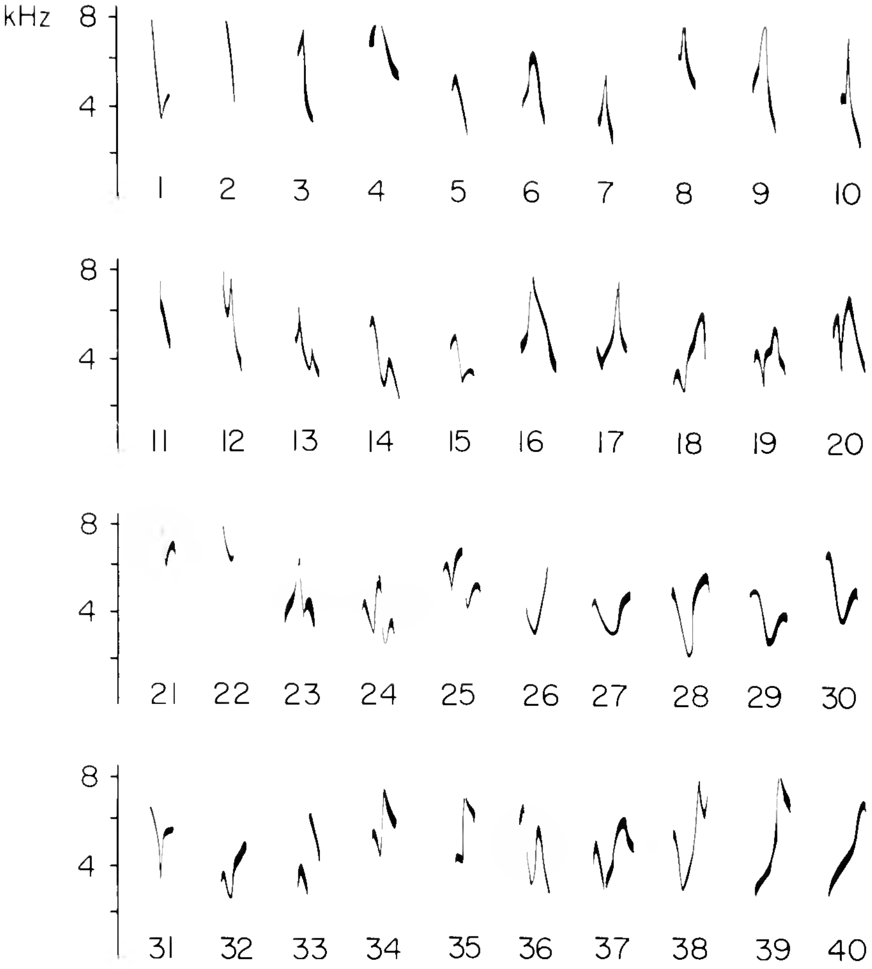

FIG. 2. Figure catalog of Yellow Warbler songs.

single bird, and by different individuals in the population. Figures that were similar, but showed consistently different form and no intermediates, were given different catalog numbers.

In Fig. 4 we have plotted the cumulative number of figures sung by a single male Yellow Warbler during a continuous series of 100 songs. The levelling off at 16 figures rather early suggests that this number represents the complete repertoire of this individual. The total figure repertoire recorded for individual males ranged from 2–27, with a mean of 8.82 (±6.10, N = 45). Almost certainly those with very small repertoires were not recorded long enough to sample all their song patterns and figures. The actual average for all individuals is therefore very likely larger than 8.82.

A cumulative plot of new song figures in all the Michigan populations with increasing numbers of consecutive individuals sampled is also shown in Fig. 4. The asymptote seems to be approached at 40 figures and 42 birds.

Fig. 5 illustrates the sharing of the various song figures among the 45 male Yellow Warblers recorded in 1974 and 1975. Some figures were

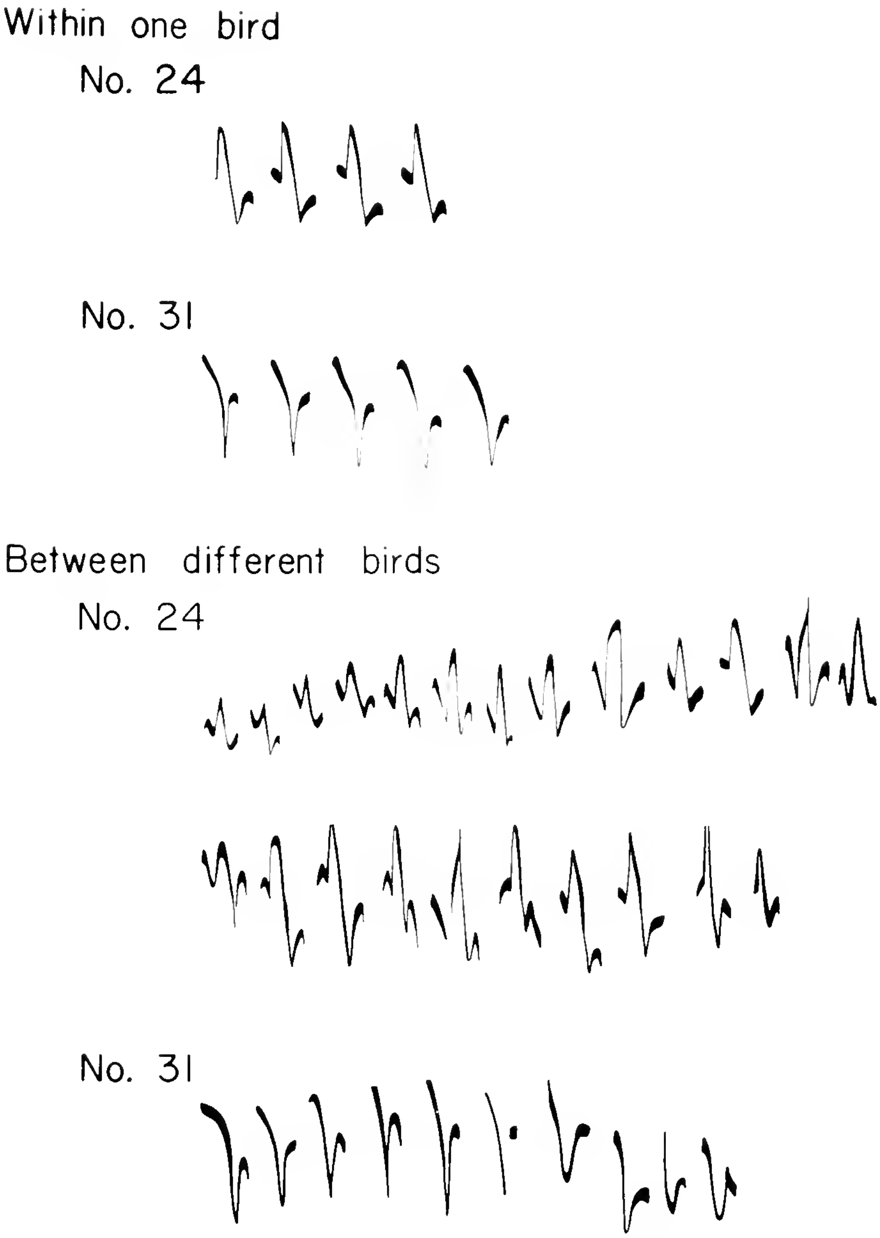

FIG. 3. Variation within song figures.

widely distributed throughout the population, but a few were sung by only 1 individual.

There was a high degree of continuity in the use of the same figures from year to year. Thirty-nine figures were recorded in 1974, while 33 were found in 1975. Of the 745 songs analyzed during the 2 years, about 60% were recorded in 1974.

Analysis of song types and song patterns.—Previous studies (Ficken and Ficken 1962, 1965, 1970; Morse 1966) have shown that the Yellow Warbler, along with some other wood warblers, has 2 principal song types. One ends with a prominent, ascending figure, e.g., 39 and 40 in Fig. 2, (Accented Ending or AE Song, Fig. 6A), while the other lacks an emphasized

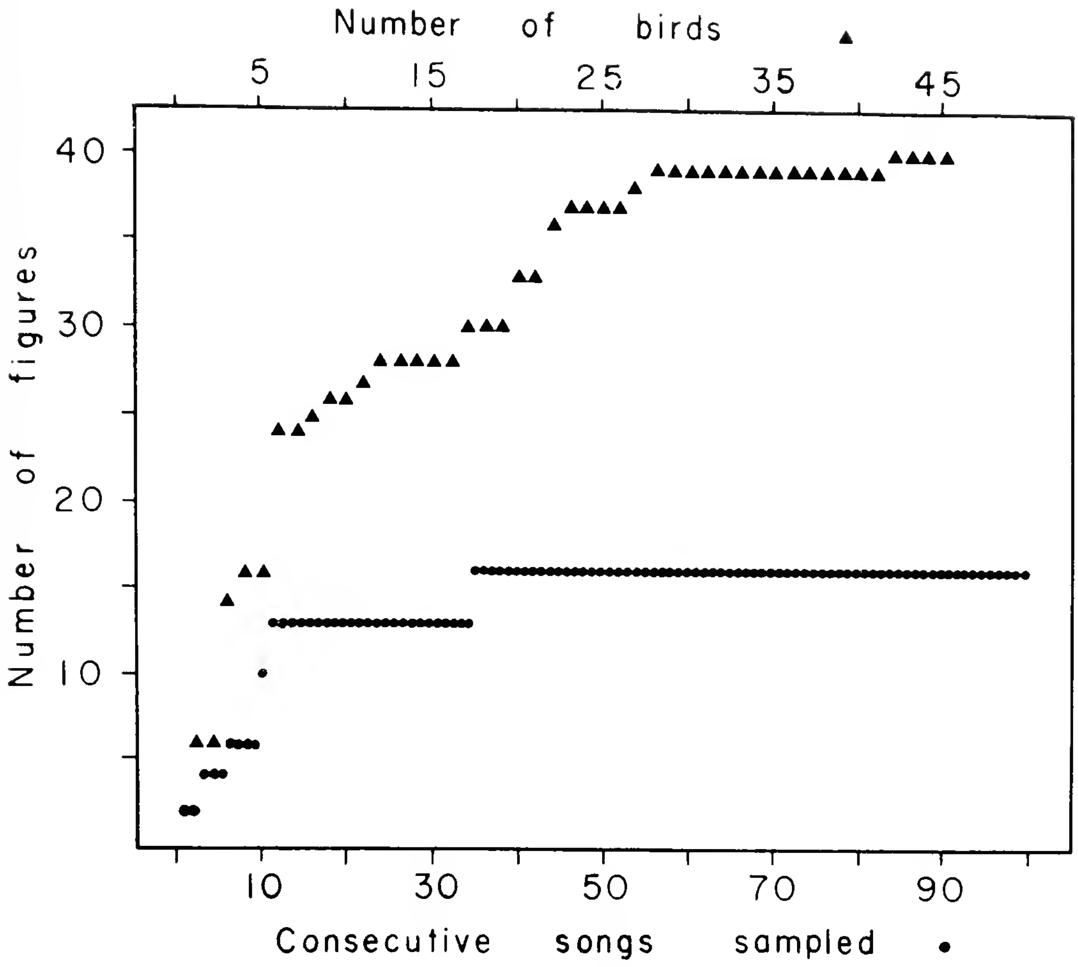

FIG. 4. Cumulative plots of the number of song figures with increase in number of birds sampled, and of the number of song figures sung during a consecutive series of songs of one individual.

ending (Unaccented Ending or UE Song, Fig. 6C,D). Morse (1966) described an additional song type sung by the Yellow Warbler, the Intermediate Ending Song. It is sung when birds change from one song type to another, and appears intermediate in motivation. Morse (1966) stated that "This song type usually has a weak upslurred accented ending, but is of an overall lackluster quality when compared to the Accented Ending Song." We did not find any songs clearly fitting this description in our recorded samples. Ficken and Ficken (1962, 1965, 1970) and Morse (1966) refer to "muted songs," either Accented Ending or Unaccented Ending song types sung at low volume in moments of extreme aggression. We found no clear examples of this in birds we observed.

In 30 Yellow Warbler songs we found a variation of the AE Song type, the Incomplete Accented Ending (IAE) Song. The IAE Song shown in Fig. 6B, had the same arrangement and kind of figures as one of the AE Songs, Fig. 6A, but lacked the ascending terminal figure. We assume that the

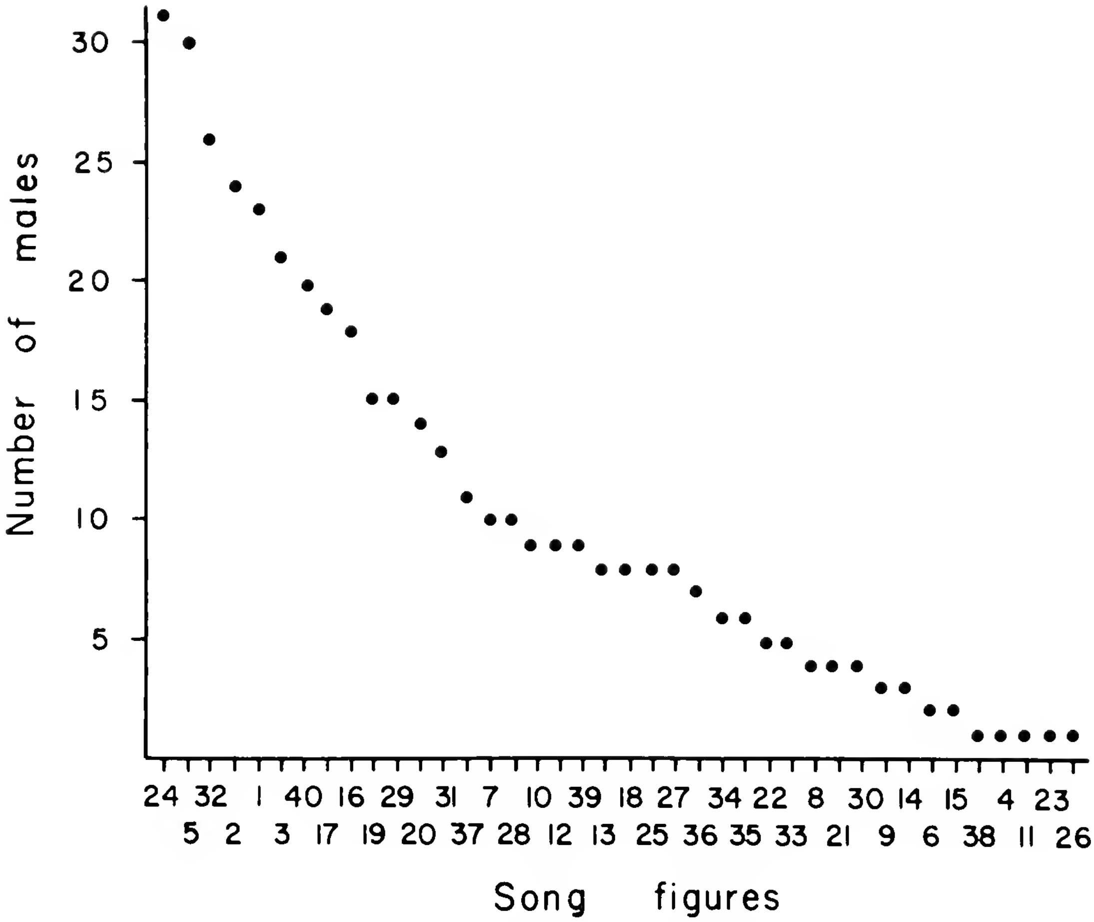

FIG. 5. The sharing of the various song figures by 45 males in 1974 and 1975.

IAE Songs represent the same song pattern as the AE, but perhaps because of lower motivation the full pattern is not sung. Singing of incomplete patterns is common, e.g., in the Indigo Bunting (*Passerina cyanea*) (Thompson 1972). The 8 males which sang these sang a similar AE Song at the same locality, general time, and date. The IAE Songs were generally interspersed among similar AE Songs, but in some cases UE Songs, of different figure composition, were also sung in the same bout. The contexts in which these similar IAE and AE songs were sung were not noted.

We distinguished 60 Unaccented Ending Song patterns and 4 AE patterns. Each of these 64 patterns had at least 1 song phrase composed of a different kind of song figure, or had the phrases arranged in a different sequence.

Song variation.—The songs of an individual differ in the arrangement, kind, and number of figures within the song. Changing the number of figures results in variation in (1) the presence or absence of certain phrases, (2) phrase length, and (3) the song ending. An individual may also alter the relative loudness of particular figures, phrases, or song patterns.

A given male sings a variety of song patterns. Male 38, recorded for 223

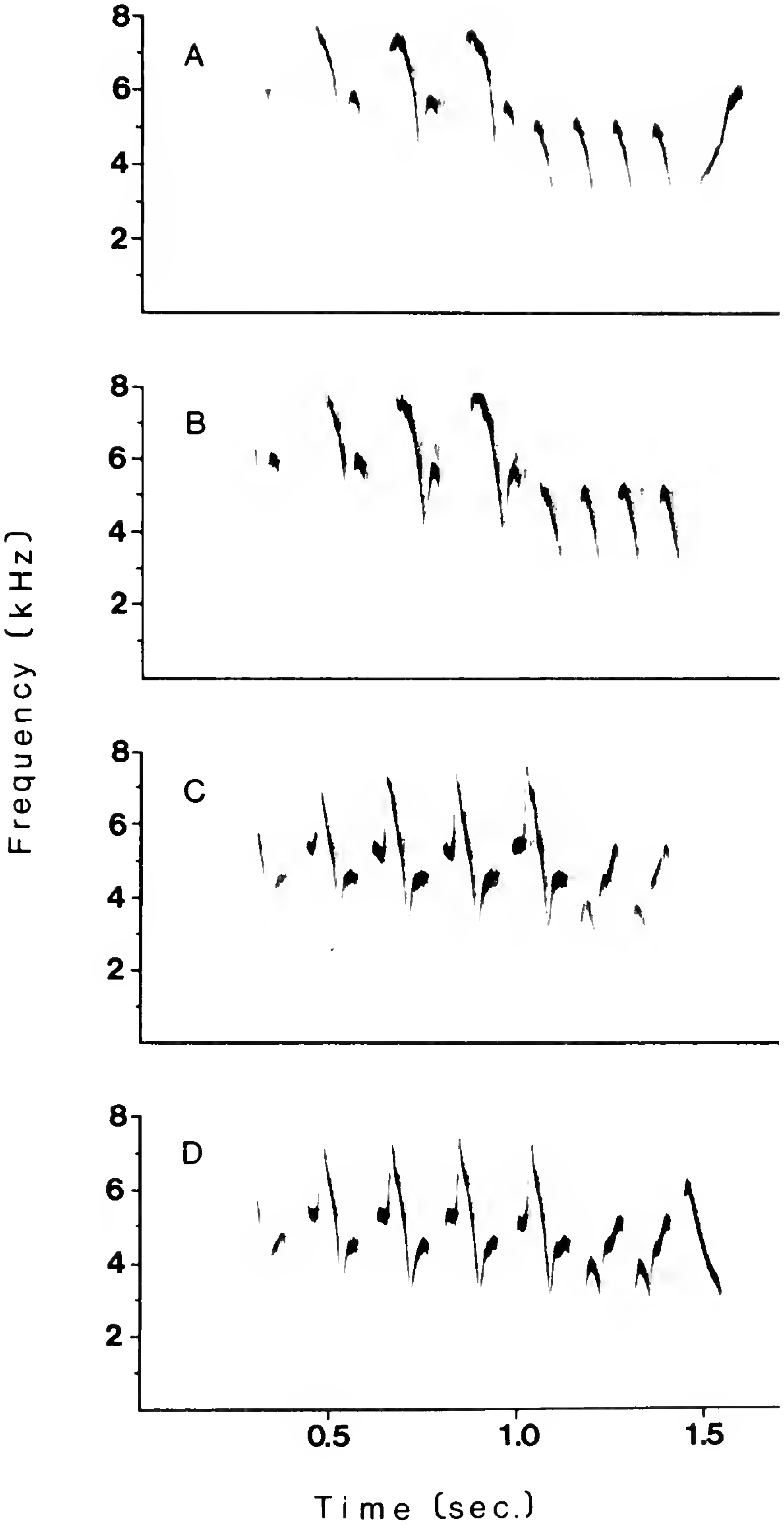

FIG. 6. Sound spectrograms of 4 typical Yellow Warbler songs.

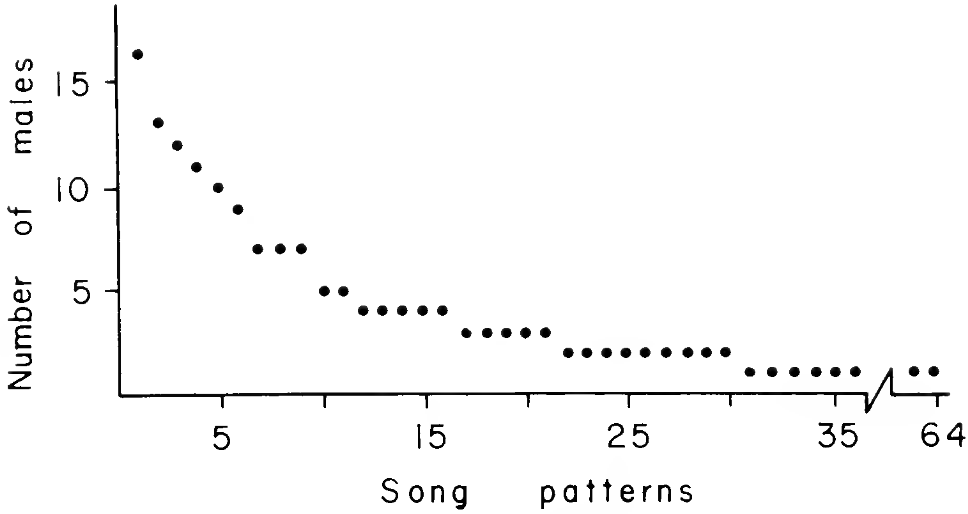

FIG. 7. The sharing of song patterns by 45 males in 1974 and 1975.

min during 4 days in July 1975 at Fort Custer, Kalamazoo Co., sang 17 different song patterns composed of 27 different figures. The number of different song patterns sung by an individual ranged from 1–16 (mean = 4.27 ± 3.36, N = 45).

There was extensive sharing of song patterns among different individuals (Fig. 7). The number of individuals singing a single pattern in the 2 years combined ranged from 1–17, with averages of 7.75 for AE and 2.65 for UAE patterns (overall mean = 2.96 ± 3.38, N = 64). Several song figures were used in different song patterns. Some figures were interchanged between AE and UAE patterns. The mean number of song patterns containing a given figure is 4.98 ± 4.46 (N = 40, range = 1–18).

An individual singing a large number of songs of a given pattern varied within that pattern. Male 17, recorded on 22 June 1974, at Coldbrook Park, Kalamazoo Co., sang a particular UE Song pattern 5 times within 5 min. During this time he sang 2 variations (see Fig. 6C,D). Song C is like song D, but lacks the descending terminal figure found in D. An individual may also vary the number of song figures per phrase. Male 3, recorded in Dearborn, sang a particular AE Song pattern 71 times on 2 June 1974. This pattern is composed of introductory, middle, and terminal phrases. The introductory phrase generally contained 5 repeated figures, but the number ranged from 3–6. Likewise, the middle phrase was usually composed of 4 repeated figures, but the number ranged from 1–4. This AE Song pattern has 1 ascending figure in the terminal phrase. The same bird altered the pattern further by omitting both the middle and terminal phrases, or just the terminal phrase.

Repetition index.—A measure of figure repetition in songs is given by the repetition index, calculated by dividing the total number of figures by

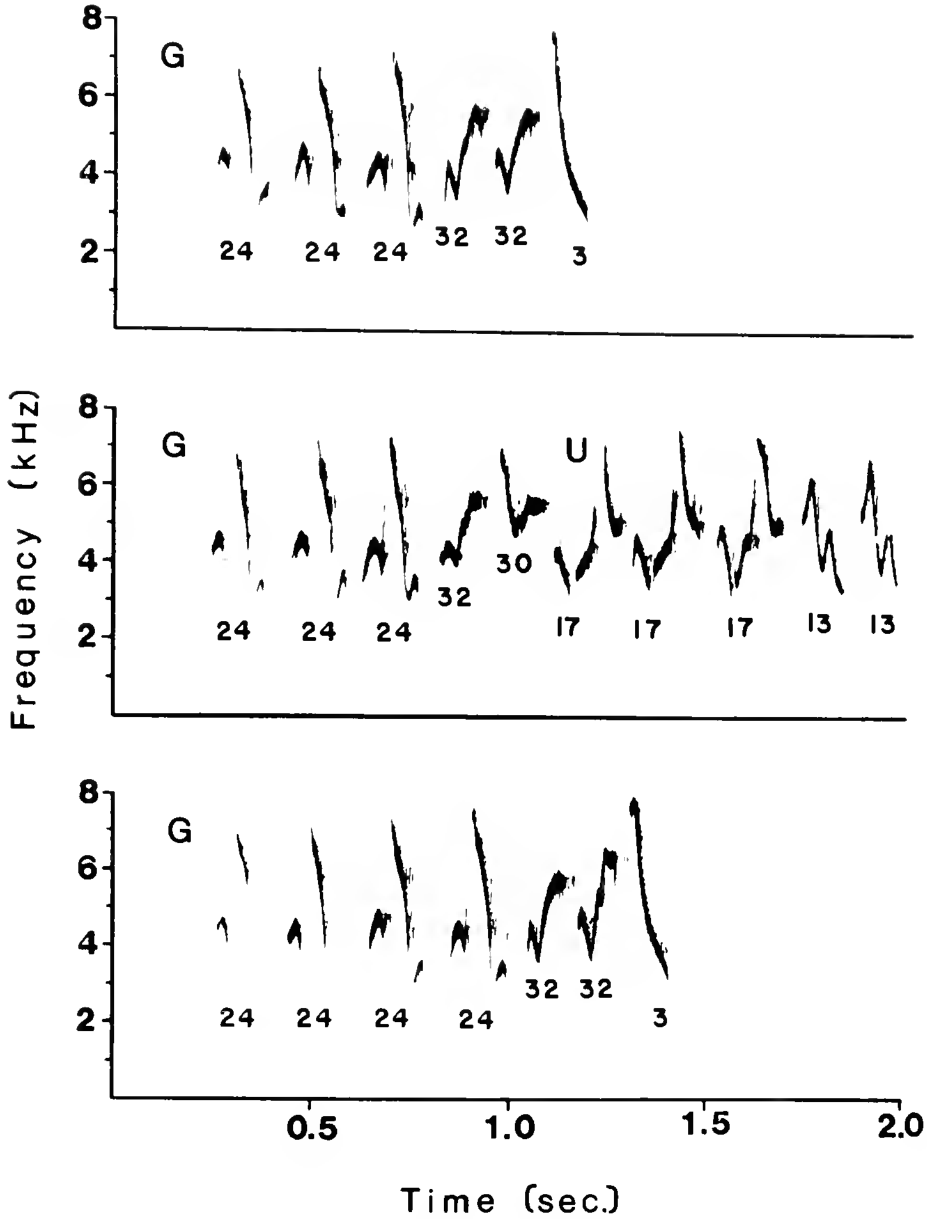

FIG. 8. Run-on song G-U with song G sung immediately before and after.

the number of kinds of figures. Repetition indices for the Dearborn population are higher than those for the XY Marsh population, in Kalamazoo County. This may be because, as already mentioned, many of the songs sung in the beginning of the breeding season when the Dearborn males were recorded are AE Songs, while many of those sung toward the end of the breeding season at XY Marsh are UE Songs. The mean repetition index for all AE Songs is 2.63, while that of UE Songs is 2.39. For both years and both types of songs together the mean number of figures per song was 6.99 ± 1.71 (N = 204), the mean number of kinds of figures per song 2.88 ± 0.92 (N = 204), and the average repetition index 2.42.

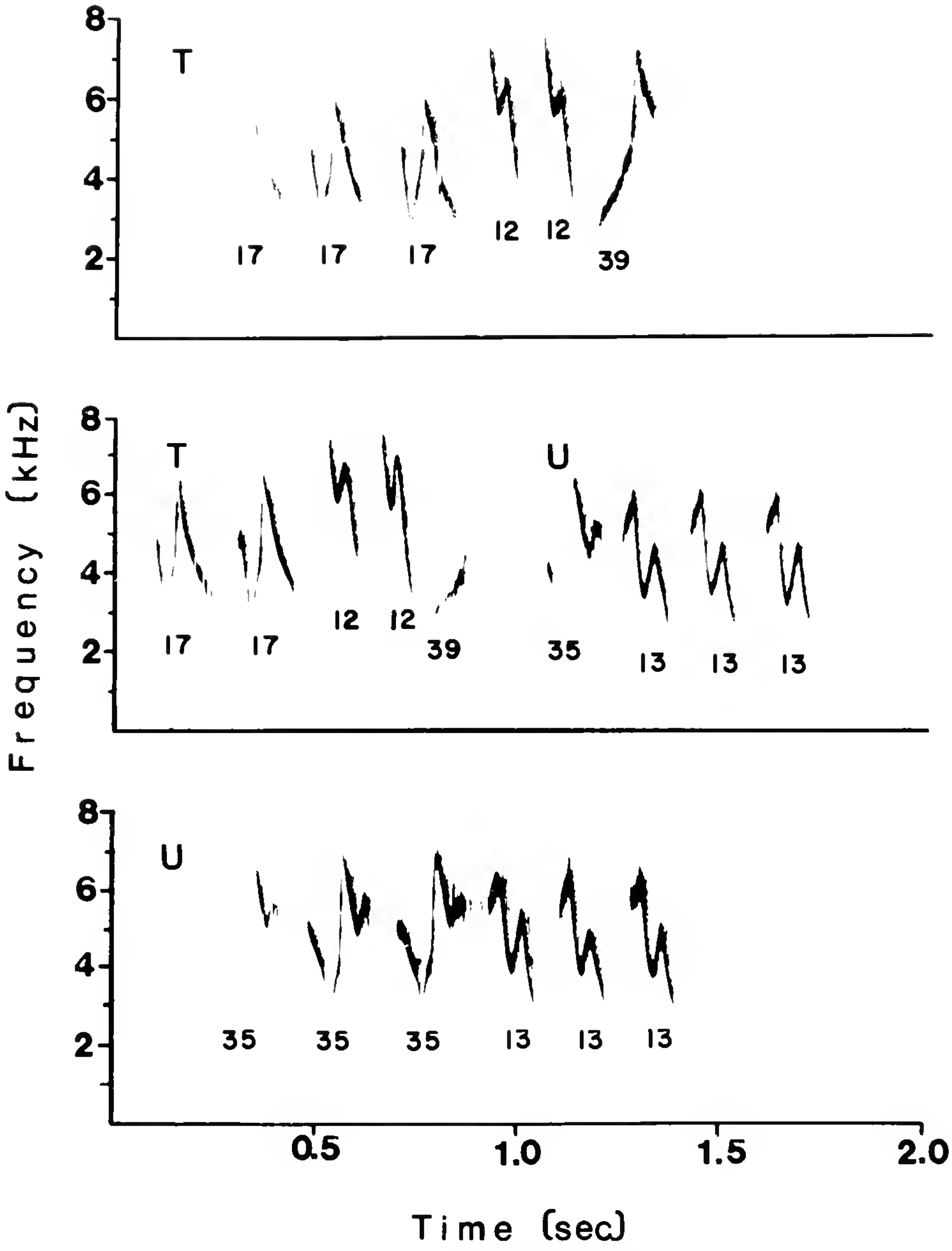

FIG. 9. Run-on song T-U with song T sung immediately before and song U after.

Run-on songs.—Six males from 4 localities sang 16 run-on songs. Thompson (1972) defined a run-on song as "a series of complete song patterns sung without break." Usually, if a bird was singing several different song patterns in a bout it simply connected any 2 to form a run-on song. However, twice new patterns not found elsewhere in the bout were used in the run-on song. Fourteen of the 16 run-on songs in our sample were composed of Unaccented Ending Songs, with no 2 UE Song patterns grouped together more than 3 times. In every case where 2 patterns were run together the second was a UE Song.

Figs. 8 and 9 show 2 sequences of run-on songs. In Fig. 8 the UE pattern

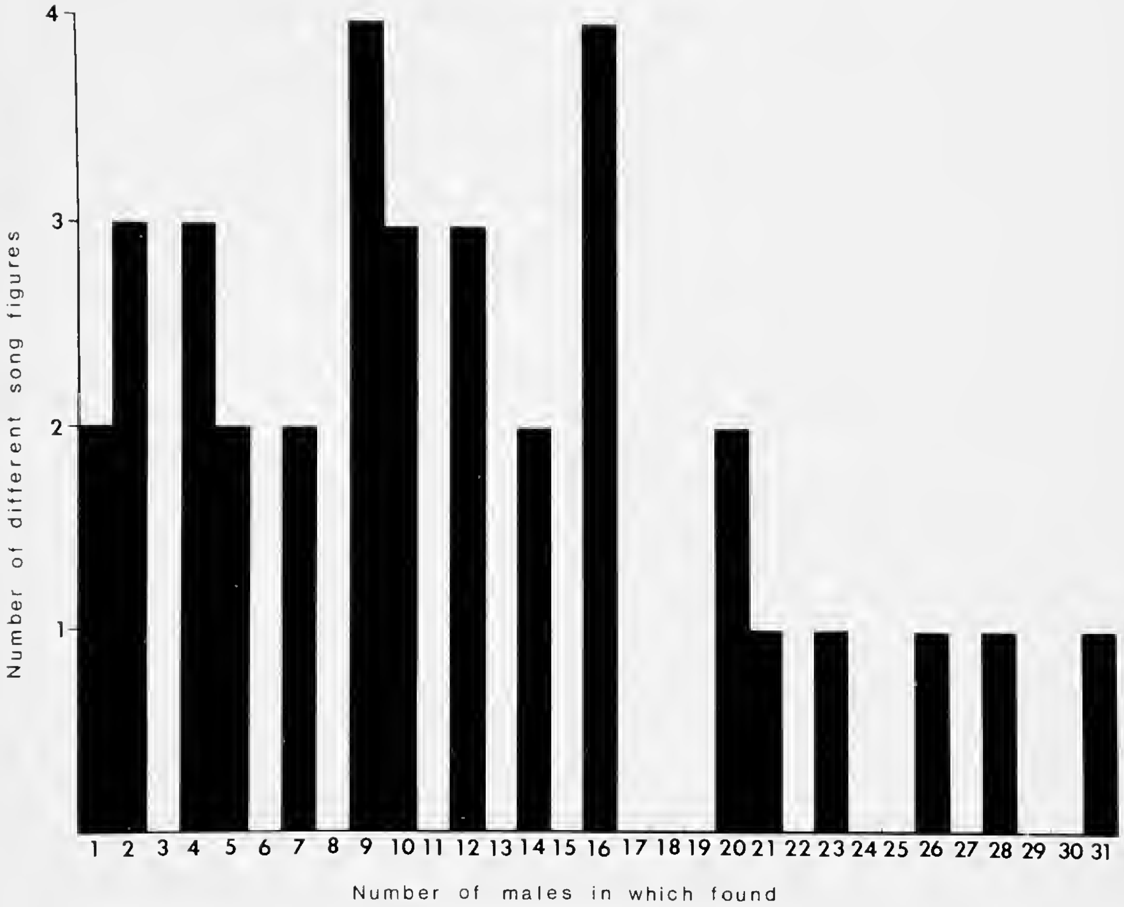

FIG. 10. Cumulative plot of the number of song patterns with increase in the number of songs sung.

G both precedes and follows the run-on song G-U. The spacing between song figures 30 and 17 that connect the 2 different UE patterns in the run-on song is no greater than the spacing between consecutive figures in either of the normal patterns. Song figure 3 found in song pattern G is omitted in the run-on song, and replaced by song figure 30. Although 30 does not appear in the other songs of this male, it appears as a terminal figure in the regular songs of 16 other individuals, and so cannot be considered peculiar to run-on songs. In contrast, the spacing between song patterns that make up AE-UE run-on songs is greater than the spacing between consecutive figures in the normal patterns. Fig. 9 shows a run-on song composed of the AE Song pattern T and the UE Song pattern U. The space between song figures 39 and 35 that connect song patterns T and U is 0.16 sec in comparison with the 0.04 sec space between song figures 30 and 17 in the run-on song of Fig. 8. Song figure 39, a terminal, ascending figure in song pattern T, is in the run-on song pattern T-U. Song figure 35 is repeated 3 times in the usual song pattern U, but appears only once in the run-on song pattern T-U.

It is possible that run-on songs are a form of individual variation associated with territorial defense. Thompson (1972) suggests than run-on songs are sung by the Indigo Bunting if a conspecific male intruder does not leave at once the resident's territory when challenged. The geographic distribution of Yellow Warbler run-on songs tends to support this hypothesis. Three of them were sung at Coldbrook Park, 4 at 44th Street, 2 at Fort Custer, and 7 at XY Marsh, all in Kalamazoo County. At each of these localities Yellow Warbler territories were small and situated in wet areas covered with heavy underbrush. Due to close proximity there would likely have been a higher incidence of intrusions, resulting in an increased number of run-on songs associated with unusually high aggressive motivation.

Geographic distribution and frequency of song-patterns.—The males inhabiting mideastern and northeastern Kalamazoo County sang approximately 5 times as many different song patterns per min as did the males recorded in Dearborn, and 3 times as many different patterns per min as did the males recorded at XY Marsh. There are 2 likely reasons why this was so. First, the Dearborn males were recorded early in the breeding season when they were singing primarily AE Song patterns. Since there are only 4 different AE Song patterns, there would not be much variety in the Dearborn males' songs. Second, the males at XY Marsh, which were recorded on a single, windy day late in the breeding season when singing was at a minimum, sang fewer songs than any of the other populations.

Although the Dearborn males sang the highest percentages of AE Song patterns, at least 1 kind of AE Song pattern was recorded in each locality sampled in southern Michigan. Between 21 May and 2 June 1974, males recorded in Dearborn sang 37.5% AE Songs and 62.5% UE Song patterns. In contrast, 3 males recorded on 7 July 1975, at XY Marsh sang for the same amount of time as did the Dearborn males, but sang only 7.7% AE Song patterns.

Fig. 10 shows a cumulative plot of the number of song patterns against the total number of songs sung. At first, the curve rises sharply, but as more songs are sampled, and increasingly larger numbers of song patterns reappear, the cumulative number of new song patterns approaches an asymptote.

The males inhabiting the marshy areas of the Fort Custer Recreation Area during the summer of 1974 sang the greatest variety of song figures. This population also shared the largest number of figures and song patterns with the other populations in southern Michigan. This could be due to the greater number of songs recorded at Fort Custer. However, the total number of songs sung by the Dearborn population in 1974 is nearly equal to

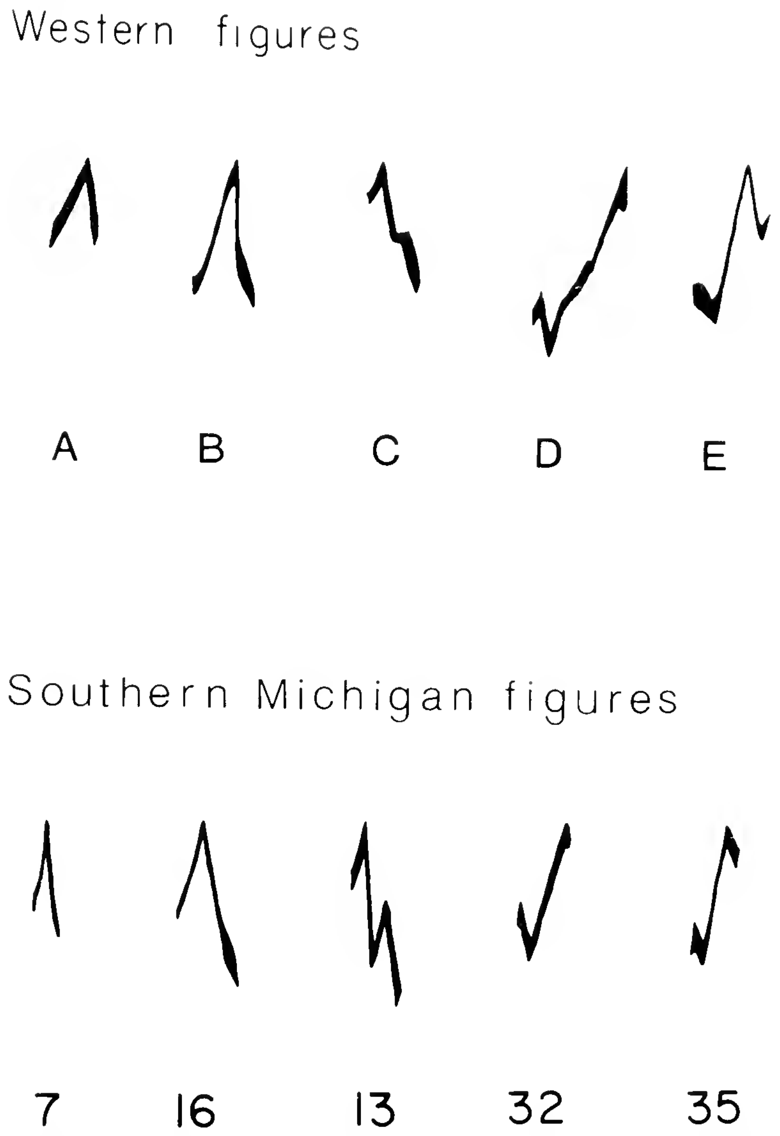

FIG. 11. Different Yellow Warbler figures sung in Nevada and California and comparable figures from southern Michigan.

the number sung by the Fort Custer population in the same year, suggesting that other factors may be important in determining the variety of song figures and song patterns. A calculation of the "overlap" of each study population with the Fort Custer figures is used to give an estimate of figure distribution. Overlap as used here is the percentage of figures found in other southern Michigan populations that are also represented in the Fort Custer-1974 population. Mideast Kalamazoo County, where Fort Custer is located, has the highest overlap (95.24%), followed by northeast Kalamazoo County (87.5%). The smallest overlap is found with the southwest Kalamazoo population (84.0%) and Dearborn (84.2%) which are farthest from Fort Custer. Nevertheless, the high overlap values found in each of the 4 main study areas, indicate a wide distribution and common

TABLE 1
FIGURE COMPOSITION OF YELLOW WARBLER SONGS

	Dearborn	Northeast Kalamazoo Co.	Mideast Kalamazoo Co.	Southwest Kalamazoo Co.
	1974–75	1974	1974–75	1975
Ave. no. of figures/song	8.18	7.15	7.02	6.00
Ave. no. of figure-types/song	3.05	2.79	2.89	2.74
Ave. repetition index	2.69	2.56	2.43	2.19

	All locations 1974	All locations 1975	Total all locations 1974–75
Ave. no. of figures/song	7.32	6.98	7.2
Ave. no. of figure-types/song	2.88	2.86	2.87
Ave. repetition index	2.54	2.43	2.5

occurrence of many figures. It is interesting that Dearborn, 170 km from Fort Custer and southwest Kalamazoo County, 34 km from Fort Custer have such similar overlap values. That may relate to the small sample size for both localities.

Songs from several individuals in the Upper Peninsula of Michigan (Boyes and Boyes 1969), New England (Kilham 1963), Nevada, and California (Gunn and Kellogg 1963) were taken from phonograph records. Figures found in both northern Michigan and New England are also found in southern Michigan. Six of 11 figures sung in Nevada and California are also sung in Michigan. Although 5 of the 11 differ from those found in northern Michigan, they are similar to certain figures in our catalog and may merely represent individual variation (see Fig. 11). There were also 5 new song patterns in these recordings. Merely changing the arrangement of figures found in southern Michigan produced the different AE Song pattern found in the New England recordings. The California recordings yielded 2 new UE Song patterns, and 2 additional AE Song patterns came from the Nevada recordings. The addition of new figures to arrangements previously recorded produced 2 of these patterns, while the other 2 resulted from rearranging figures that are found in the southern Michigan catalog and adding new ones.

Song length in terms of the average number of figures per song varied slightly among the 4 major study areas (see Table 1). Data for 1974 and 1975 reveal that the Dearborn population, recorded earliest in the season, has the highest average number of figures per song, while the XY Marsh population, recorded last, has the lowest. Data on the average number of kinds of figures per song show a similar pattern.

DISCUSSION

The song figures of the Yellow Warbler seem to maintain stability of form over time and over considerable geographic distances. The high overlap values among the song figures obtained from Fort Custer in 1974 and the other areas within Kalamazoo County, southeastern Michigan and other areas of the United States, confirm the extent of this stability. Borror (1967) found that in the Common Yellowthroat (*Geothlypis trichas*) a particular "phrase type" has a range of between 200 and 460 km. Similarly, Shiovitz and Thompson (1970), Emlen (1971), and Forsythe (1974) noted extensive geographic distribution of song figures in the Indigo Bunting.

The Yellow Warbler used various combinations of 40 figures to produce 64 different song patterns. In comparison, Shiovitz and Thompson (1970) found that the Indigo Bunting has about 118 figures, and Borror (1967) found that the Common Yellowthroat has 83 "notes" (figures). Shiovitz and Thompson (1970) calculated that even with a song length of 5 figures, a limited repertoire of 100 figures, and no repetition, a total of over 9 billion different song patterns is theoretically possible. Substituting the corresponding values for the Yellow Warbler (an average of 2.87 figure types per song and a total repertoire of 40 figures) results in a theoretical total of over 59,000 different song patterns. In actuality, the number of possible song patterns is more limited, because certain figures tend to appear either at the beginning or end of the song.

Probably a combination of several interrelated factors results in the Yellow Warbler's having so many UE (60) and so few AE (4) songs. We found, as did Morse (1966), that the AE Song patterns are sung mostly prior to and during pair formation, while the UE Songs are sung toward the end of the breeding season, following pair formation, and along territorial boundaries. Morse (1966) states that the "Accented Ending Songs were almost always given in the presence of female Yellow Warblers." According to Ficken and Ficken (1965) "the Accented Ending Song is more attractive to conspecific females than the" Unaccented Ending Song. The less variable AE Song would permit fast recognition by a female of the same species. Ficken and Ficken (1962) found that the AE Songs of the Yellow Warbler were strikingly different from AE Songs sung by other species of warblers belonging to the same genus, while the UE Songs of the Yellow Warbler were quite similar to those of the Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*Dendroica magnolia*), and American Redstart (*Setophaga ruticilla*). Ficken and Ficken (1965) found that the AE Songs, in at least 2 species of *Dendroica*, seemingly functioned in maintaining reproductive isolation. Morse (1966) thought AE Songs of male Yellow Warblers both attracted conspecific females and discouraged intrusion of males of other species. We are uncertain why songs unlike their own should discourage males of other species from intruding. It would seem more logical for UE Songs, resembling the songs of other species, to serve this function. Ficken and Ficken (1965) also associate AE Songs with success in territorial defense, and UE Songs with escape tendencies. Lein (1972), in a dissenting view, concluded that AE Songs in the Black-throated Green Warbler (*D. virens*) are sung under the influence of a high androgen level, in the breeding habitat, and in the absence of conflicting external inputs. He found that males sing UE Songs in the presence of another male, when on insecure ground, or at low light levels. Our data are not sufficient to resolve these differences of opinion.

If species identification is a prime function of AE Songs, then this function would be served by the small number of patterns we find, making identification simpler. In contrast to the small number of AE Songs, the 60 different UE Song patterns represent a much greater variability. After pair formation, the stability of song patterns that facilitates species recognition and mating seems to become less important than song variation which allows the Yellow Warbler to be recognized as an individual. The UE Song patterns are sung predominantly along territorial boundaries to male conspecifics (Ficken and Ficken 1965, Morse 1966, Lein 1972). The variety of UE Song patterns would allow the territorial male to differentiate between the songs of a territorial neighbor and a stranger. From an ecological point of view, once territorial boundaries are established, a bird can conserve energy by not responding to a neighbor's song (Falls 1969).

The only other parulid that regularly occupied Yellow Warbler habitat in this study was the Common Yellowthroat. The temporal arrangement of the Common Yellowthroat's song is clearly different from the Yellow Warbler's UE Song. The average song length and repetition index of the Common Yellowthroat song in various Michigan localities was 1.75 and 3.33 sec, respectively, and its rhythmic characteristics are quite different. Borror (1967) found that the frequency range of most Common Yellowthroat songs that he recorded was 4.00 kHz. This is much different from the Yellow Warbler's UE Song, which on the average is shorter (1.30 sec), has a lower repetition index (2.50), and a higher frequency (5.10 kHz). In addition, the "notes" (=figures) of the Common Yellowthroat, as described by Borror (1967), consisted of simple slurred elements, having no rapid frequency modulation. The Yellow Warbler figures are generally short in duration (narrow) and have a rapid frequency modulation. The songs of the 2 species thus serve as clearly distinctive epigamic and intrasexual displays.

SUMMARY

During May, June, and July 1974 and 1975, 47 male Yellow Warblers (*Dendroica petechia*) from 9 localities in southern Michigan were observed and 1328 songs from these populations

recorded. Spectrographic analysis of 745 songs yielded 40 different types of figures arranged in various combinations to form 4 Accented (AE) and 60 Unaccented Ending (UE) song patterns.

Song variation in individual males resulted from variation in the number, arrangement, and kind of figures, deletion or addition of phrases, or change in arrangement of phrases within the song pattern. Twelve of the 14 song patterns that were combined to form 16 run-on songs were UE Song patterns.

The average number of kinds of figures per song was 2.87. A greater percentage of AE Songs was sung toward the earlier part of the breeding season, while more UE Songs were sung toward the end. Differences in the repetition indices between localities seemed to be based on this difference in seasonal behavior. Thirty-nine of the 40 different figures were recorded in 1974 and 33 in 1975. The mean number of song patterns containing a given figure was 4.98. High overlap values (84.0%–95.2%) for figure composition of songs were found in all the southern Michigan populations studied.

Furthermore, 19 of the 24 figures found in songs recorded in 3 separate areas in the U.S. were the same as those found in southern Michigan. This suggests that the figures sung by the Yellow Warbler are limited in number and maintain great stability of form.

ACKNOWLEDGMENTS

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NEW LIFE MEMBER

Mrs. Betty Darling Cottrille is an avid photographer/ornithologist, who has recently become a Life Member of The Wilson Ornithological Society. For many years she and her husband have been studying North American Warblers, flycatchers and vireos on their breeding grounds, and have on occasion contributed to the literature. Mrs. Cottrille has also published on the distribution of the Piping Plover (*Charadrius melódus*) in Michigan, and has co-authored a study on the Great Blue Heron (*Ardea heródias* L.). In keeping with her interests as a photographer Mrs. Cottrille has also presented slide programs of her work. Besides being a member of a number of ornithological/naturalist societies Mrs. Cottrille is, by avocation, a pianist.

Wilson Bull., 91(4), 1979, pp. 551–574

VOCALIZATIONS AND BEHAVIOR OF THE WILLET

Tex A. Sordahl

While the vocal repertoires of several game species have been analyzed spectrographically (Collias and Joos 1953, Ellis and Stokes 1966, Stokes 1967, Williams 1969, Heinz and Gysel 1970, Samuel and Beightol 1973), other non-passerines have been largely neglected. The shorebirds (Charadrii) provide a possible exception. The flight-song has frequently been discussed in shorebird studies because of its importance in territorial behavior, and has been analyzed in detail by Heidemann and Oring (1976). Some recent studies have presented spectrographic analyses of the whole vocal repertoire of single species (Oring 1968, Forsythe 1970, Bursian 1971, Graul 1974, Jenni et al. 1974, Skeel 1978). This paper presents a spectrographic analysis of Willet (*Catoptrophorus semipalmatus*) vocalizations and describes their importance in the bird's biology. It includes comments on their etiology, functions and adaptiveness.

STUDY AREA AND METHODS

I studied Willets during 2 breeding seasons (June 1974 to August 1975), totalling over 400 h of observation. Additional observations were made in 1976, 1977 and 1978.

The principal study site, located ca. 3 km west of Amalga, Cache Co., Utah, consists of a seasonally wet alkali flat known as The Barrens. In the midst of The Barrens is a series of broad, shallow (≤ 0.5 m deep) ponds. Surrounding these artifically maintained Barrens' ponds are drier fields and pasturelands. Some additional observations were made on Willets in other parts of Cache Valley and at the Bear River Migratory Bird Refuge in Box Elder County, Utah.

Field observations were made with 7 × 35 binoculars and a 20× spotting scope, often from an automobile or portable blind. Vocalizations were recorded at a tape speed of 19 cm-sec^{-1} on a Sony TC-800B portable tape recorder with a F-26S cardioid microphone mounted on a 61-cm parabolic reflector. Spectrographic analysis was done at the FL-1 setting on a model 6061-B Kay Electric Company Sona-Graph. A Tandberg Model 15-41F tape recorder was used with the sonagraph. Frequency measurements were taken from spectrograms made at the narrow band-pass setting, and temporal measurements were taken from spectrograms made at the wide band-pass setting. All time-frequency displays used in the analysis were made at a normal playback speed of 19 cm-sec^{-1}, but some made at 9.5 and 4.8 cm-sec^{-1} were used to clarify temporal patterning of notes. The acoustical terminology of Davis (1964) is followed.

Since no adults could be color-marked, long-term recognition of individuals was impossible. However, some individuals could be followed for several hours on a given day. Accordingly, an effort was made to use recordings from scattered locations in the study area for the numerical analysis (Table 2) so the standard deviations would represent interindividual variability within the population. As with Tomkins (1965), I found no reliable way to distinguish the sexes other than by behavior.

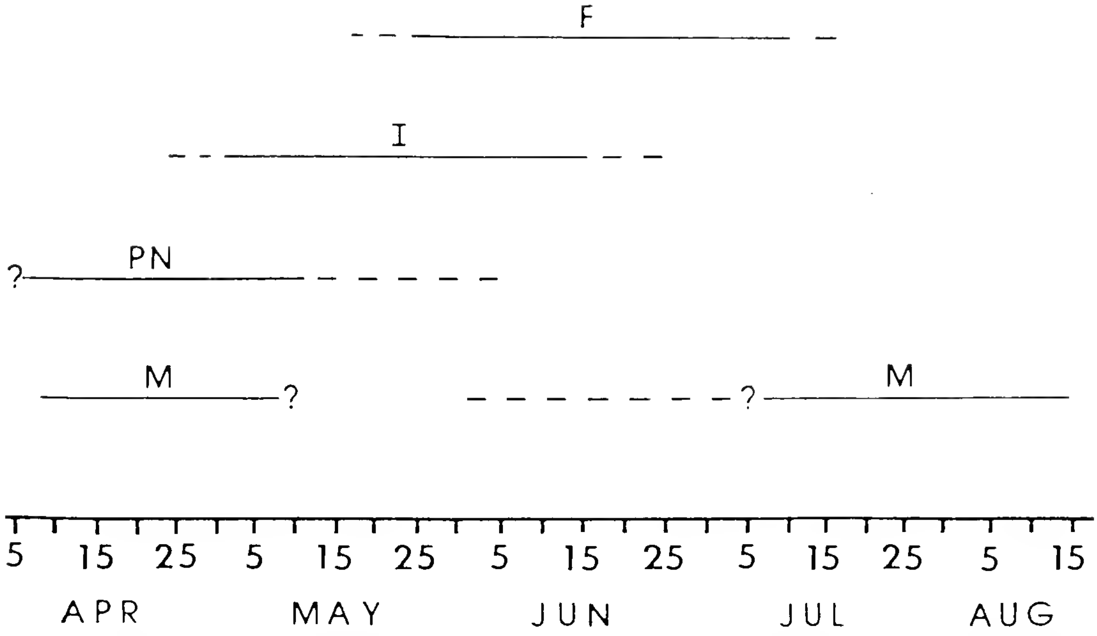

FIG. 1. Breeding schedule of the Willet in Cache County, Utah. (M = migration; PN = pre-nesting; I = incubation; F = fledgling care. Solid lines indicate periods based on observations; dashed lines indicate possible extensions based on calculations.)

RESULTS

Willets arrived in Cache Valley during the first week of April, with first arrivals seemingly paired. The breeding schedule of this population is presented in Fig. 1. Calls and their biological characteristics are summarized in Table 1, and a quantitative description is presented in Table 2. A discussion of each vocalization follows.

Pill-will-willet.—This loud and ringing call (Fig. 2A), from which the bird derives its common name, consists of 3 parts: *pill-*, which is a stuttered series of 3 to 5 ($\bar{x}$ = 3.30, SD = 0.46, N = 66) short notes, is separated from *-will-* by about 0.03 sec, and *-will-* is separated from *-willet* by about 0.04 sec. Once a bird consistently gave this call with the *wil-let* broken, and 2 birds gave it without the terminal syllable (hence, *pill-will-will*). The call has a harmonic structure with the fundamental (at about 1.1 kHz) and odd harmonics suppressed. The first overtone is emphasized.

This call has been likened in function to passerine song (Vogt 1938). If song is defined as "advertising the presence of a paired or unpaired male in breeding condition, as well as the existence of a defended territory" (Nottebohm 1975), it should be considered song. Vogt (1938) ascribed this call primarily to males, and I only heard it a few times from known females. On 1 May 1975, a female gave this call as a male approached her sexually (a successful copulation ensued). Evidence for an advertising function is given by the fact that Willets often gave this call in the absence of any obvious recipient or external stimulus. Von Frisch (1960, *in* Arm-

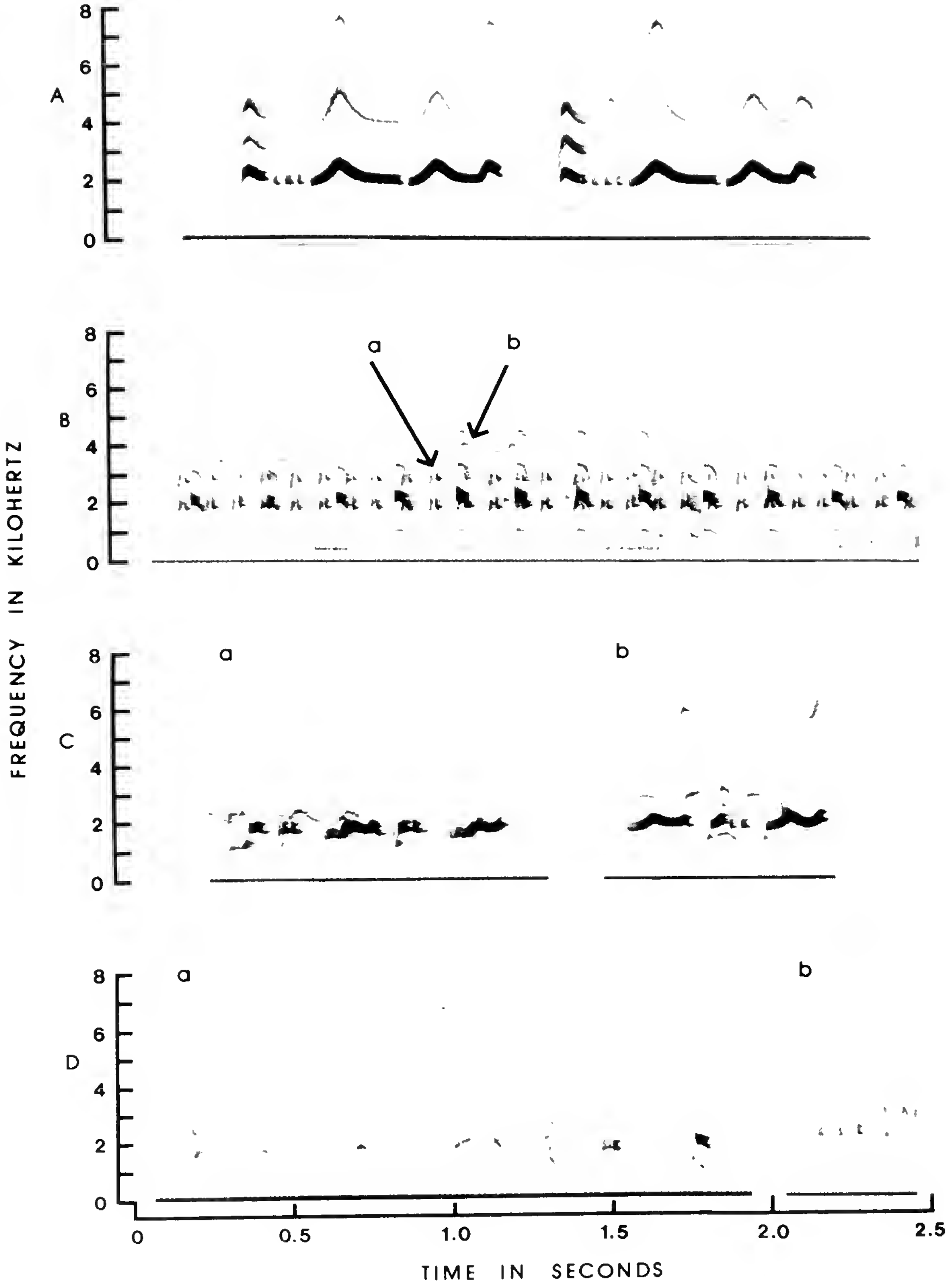

FIG. 2. Spectrograms of Willet vocalizations. A. Two *pill-will-willet* calls; B. a, *klik* calls and b, *dik* calls given simultaneously by 2 birds (see text); C. a, b, 2 examples of *hunker-hunk*; D. a, b, 2 examples of *cluck*.

TABLE 1
SYNOPSIS OF THE CALLS OF THE WILLET

Call	Sex of bird	Occurrence during annual cycle[a]	Etiology	Simultaneous behavior[c]	Function
Pill-will-willet	Both	PN through late F	Presence of conspecifics or disturbance on territory	*A* display; *T* wing-up display; erect stance	Proclamation of territory and mate; announcement
Klik	Male?	PN	Second Willet in proximity	*T* wing-flutter display	Epigamic
Dik	Female?	PN	Sexual approach of male Willet	Horizontal posture or walk/run away	Epigamic
Kyah-yah 1-, 2-, 3-, and 4-note variants	Both	Probably AY	Presence of conspecific	*T* activities (feeding, comfort); flight or taking flight	Contact, flight intention, flight enticement
Kleep high, medium, and low intensity	Both	Probably AY	Disturbance of individual, especially with respect to nest or young	Flight; *T* head-bobbing display; mobbing	General predator alarm
"Scream"	Both	Probably AY	Active presence of an enemy	Flight or taking flight; mobbing	Excitement
Cluck	Both	Probably AY	Conspecific in proximity	Flap-hop or wing-up display, or pause in *T* activity	Distance increaser
Hunker-hunk[b]	Both	Possibly AY	Some disturbance in the vicinity	Most often given on ground	?
"Warble"[b]	?	F?	Presence of potential predator in vicinity of young	Alert posture; young crouch?	Warning to young?
"Whistle"[b]	?	F?	?	Circling flight	?
Eeee	Both (Young)	F	Imminent danger to self	Active escape attempts	Distress

TABLE 1
CONTINUED

Call	Distance decreaser	Associated calls	Elicited by conspecifics	Answered by conspecifics	Calls given by conspecifics
Pill-will-willet	No	*Hunker-hunk, kleep*	Yes	Yes	*Pill-will-willet, hunker-hunk, kleep*
Klik	Yes	*Pill-will-willet, kleep*	Yes	?	*Dik*
Dik	?	*Pill-will-willet, kleep*	Yes	?	*Klik*
Kyah-yah 1-, 2-, 3-, and 4-note variants	Yes	*Kyah-yah* variants, *cluck*	Yes	Yes	*Kyah-yah* variants
Kleep high, medium, and low intensity	Yes	"Scream," *pill-will-willet*	Sometimes	Yes	*Kleep, pill-will-willet,* "scream"
"Scream"	No	*Kleep, pill-will-willet*	Sometimes	Sometimes	"Scream", *kleep, pill-will-willet*
Cluck	No	*Kyah-yah* variants	Yes	Yes	*Cluck, kyah-yah* variants
Hunker-hunk[b]	No	*Pill-will-willet, kleep*	Yes	Yes	*Pill-will-willet, kleep*
"Warble"[b]	?	*Pill-will-willet*	Probably not	No	?
"Whistle"[b]	?	?	Probably	?	?
Eeee	Yes	?	No	Yes	*Kleep,* "scream"

[a] PN = pre-nesting, F = fledgling, AY = all year.
[b] See text for further explanation.
[c] *A* = aerial, *T* = terrestrial.

TABLE 2
NUMERICAL DESCRIPTION OF WILLET VOCALIZATIONS

Call	N	$\bar{x}$	±SD
Pill-will-willet			
Duration of call[a]	68	0.785	±0.039
Interval between calls	56	0.201	±0.088
Maximum frequency[b]	69	2.46	±0.09
Minimum frequency	69	1.79	±0.07
Klik			
Duration of call	64	0.037	±0.006
Interval between calls	57	0.056	±0.016
Average fundamental frequency[c]	45	1.03	±0.05
Average emphasized frequency	64	2.04	±0.05
Dik			
Duration of call	51	0.037	±0.012
Interval between calls	45	0.113	±0.044
Average fundamental frequency	43	1.16	±0.05
Average emphasized frequency	51	2.16	±0.06
Kyah-yah			
1-note variant			
Duration of note	15	0.301	±0.090
Interval between notes	3	0.677	±0.206
Average fundamental frequency	5	1.16	±0.05
Average emphasized frequency	14	2.24	±0.14
2-note variant			
Duration of first note	16	0.221	±0.083
Duration of second note	16	0.167	±0.049
Interval between first and second notes	16	0.051	±0.024
Duration of call	16	0.439	±0.137
Interval between calls	4	0.657	±0.326
Average fundamental frequency of first note	7	1.23	±0.10
Average emphasized frequency of first note	16	2.27	±0.12
3-note variant			
Duration of first note	18	0.139	±0.061
Duration of second note	18	0.125	±0.036
Duration of third note	18	0.119	±0.039
Interval between first and second notes	18	0.043	±0.028
Interval between second and third notes	18	0.044	±0.030
Duration of call	19	0.472	±0.140
Interval between calls	2	0.445	±0.035
Average emphasized frequency of first note	17	2.33	±0.14

TABLE 2
CONTINUED

Call	N	$\bar{x}$	±SD
4-note variant			
Duration of first note	5	0.136	±0.054
Duration of second note	5	0.140	±0.044
Duration of third note	5	0.118	±0.027
Duration of fourth note	5	0.114	±0.029
Interval between first and second notes	5	0.038	±0.024
Interval between second and third notes	5	0.046	±0.032
Interval between third and fourth notes	5	0.044	±0.026
Duration of call	5	0.630	±0.209
Interval between calls	2	0.695	±0.177
Average emphasized frequency of first note	6	2.30	±0.14
Kleep			
High intensity = interval < 2 × duration			
Duration of call	58	0.113	±0.041
Interval between calls	52	0.146	±0.052
Average fundamental frequency	55	1.29	±0.06
Average emphasized frequency	60	2.48	±0.13
Medium intensity = 2 × duration ≤Interval < 3 × duration			
Duration of call	63	0.094	±0.023
Interval between calls	58	0.229	±0.054
Average fundamental frequency	32	1.25	±0.07
Average emphasized frequency	67	2.37	±0.10
Low intensity = interval ≥ 3 × duration			
Duration of call	52	0.092	±0.017
Interval between calls	44	0.323	±0.073
Average fundamental frequency	38	1.31	±0.03
Average emphasized frequency	56	2.48	±0.10
"Scream"			
Attack			
Duration of call	38	0.191	±0.098
Interval between calls	33	0.183	±0.114
Average fundamental frequency	6	1.30	±0.00
Average emphasized frequency	38	2.50	±0.19
Flee			
Duration of call	26	0.348	±0.059
Interval between calls	21	0.200	±0.056
Average emphasized frequency	23	2.42	±0.08

TABLE 2
CONTINUED

Call	N	$\bar{x}$	±SD
Cluck			
Duration of notes	49	0.059	±0.015
Interval between notes	44	0.095	±0.089
Average fundamental (= emphasized) frequency	53	1.42	±0.18
Hunker-hunk			
Duration of individual notes	28	0.147	±0.067
Interval between individual notes	20	0.136	±0.157
Duration of note clusters	6	0.570	±0.183
Maximum frequency	8	2.06	±0.14
Minimum frequency	8	1.55	±0.19
"Whistle"			
Duration of first note	9	0.128	±0.004
Duration of second note	9	0.124	±0.005
Interval between notes	9	0.080	±0.016
Duration of call	9	0.334	±0.010
Interval between calls	9	2.84	±2.03
Maximum frequency	9	4.53	±0.14
Minimum frequency	9	3.39	±0.26
Eeee			
Duration of call	24	0.527	±0.080
Interval between calls	17	0.321	±0.128
Average frequency	24	4.56	±0.13

[a] All durations and intervals are in sec.
[b] All frequencies are in kHz.
[c] Average frequencies were determined by estimation of the frequency on either side of which lies half of the sound energy.

strong 1963) noted that the song-flights of a number of shorebirds may be elicited by different types of stimuli and might be termed "excitement flights." All authors have recognized the territorial function of *pill-will-willet*. When on territory, birds frequently gave this call (occasionally accompanied by a wing-up display) when another Willet flew by. Often the caller gave chase, especially if the intruder landed nearby.

I concur with Tomkins (1965) that this call is given frequently during the day or (occasionally) night during the pre-nesting period, less so during incubation, and only occasionally while escorting young. *Pill-will-willet* may be uttered from the ground or in flight. Howe (1974) noted that males and females (at least when a male is present) gave this call after landing in the territory and while holding both wings vertically for 2 or 3 sec.

Aerially, this call is given in song-flight (*sensu* Armstrong 1963: 136), a conspicuous performance which Vogt (1938) dubbed "spottying" because of its resemblance to the flight of the Spotted Sandpiper (*Actitis macularia*). This display is characterized by stiffly arched wingbeats which pass through a shallow arc (producing a hovering effect), alternating with periods of gliding on outstretched wings. It may occur at heights from about 10 m to those that make the Willet a mere speck to a human observer. The bird calls persistently, and there is no relationship between the undulating pattern of flight and the syllable delivered, as there is in the song-flight of the Red Knot (*Calidris canutus*) (Nettleship 1974). The performance is often terminated by a spectacular earthward swoop on outstretched wings. Sometimes the bird is silent during the final few meters of descent (Vogt 1938, pers. obs.) but, just as often, calling continues until the bird has landed and given a wing-up display. *Pill-will-willet* is sometimes given during direct flight, but even then it is usually alternated with the display flight. Its intermittent occurrence during mobbing sequences suggests that during times of stress it may be given as a displacement call. Alternatively, it may be released by the sight of other Willets that have joined the mob in the territory (I could never determine positively if it was the resident calling). As noted by Vogt (1938) this song-flight is highly contagious among neighboring Willets. When 1 bird began the display, up to 6 more Willets often were stimulated to do likewise. These cacophonous events were interjected between periods of silence. The birds flew in wide circles roughly delimiting their territories (on the order of 0.04 km^2), although they gravitated toward the nearest displaying neighbor. Sometimes a bird continued in a straight line until out of sight, crossing several territories as it went. Willet singing bouts sometimes lasted 5 min or more during the pre-nesting period, an individual engaging in 5 or more bouts per h.

Klik and dik.—These 2 calls (Fig. 2B) were transliterated to reflect their staccato nature and the fact that *klik* is a double-noted call and *dik* is a single-noted call. They are of approximately the same duration and frequency, but *klik* is repeated nearly twice as rapidly as *dik* (Table 2). Both have a harmonic structure, with the second harmonic emphasized.

Klik and *dik* were heard exclusively during copulation attempts (51 observations). Many of my recordings of these calls are of poor quality, but it seems that both calls were always given in such situations, even when mounting did not occur. The 2 calls were difficult to distinguish by ear, except when *dik* calls became very loud.

The literature is vague concerning the epigamic calls of Willets. The description by Nichols (1920) of a "kuk-kuk-kuk . . . in tern-like series from two mating birds" has been followed in later accounts (e.g., Bent

1929). Vogt (1938) described a rapid clicking which increased in tempo as the "male copulation note" and a "grunting eh-eh note" given by the female during copulation. Sonagrams reveal 2 structurally different notes which are out of phase. In 2 cases where it was possible to analyze recordings of copulation attempts from beginning to end, the sequence began with *klik* calls. Both ended with *dik* calls, grading into *kleep* calls. As neither resulted in mounting, I have inferred that *klik* was produced by the male (who appeared to initiate the episode) and that *dik* was produced by the female. However, even though females can be seen to open their bills at irregular intervals during copulation, the possibility that males produce both *klik* and *dik* with separate sound sources cannot be excluded without further evidence. The augmentation of the *klik* calls by *dik* calls explains the increase in tempo mentioned by Vogt (1938) as well as the pulsed sensation a listener receives (analogous to the beats produced by 2 simple tones of slightly different frequencies).

These calls may be repeated for up to 2 min or more as a male pursues an unreceptive female. Males employ a precopulatory wing display which has been called "wing-flickering" (Vogt 1938) or "wing-waving" (Tomkins 1965). Both the wing display and the copulatory notes are given until the act is completed. Near the end of the actual copulation, *dik* calls become louder and more irregular, often grading into *kleep* calls.

An interesting feature of Willet copulation notes is their conspicuousness. Vogt's (1938) statement that they could be heard at distances exceeding ⅛ mile (0.20 km) is accurate. I estimated that at times they could be heard at twice that distance. It is unusual for a bird to make itself so conspicuous at such a vulnerable time—one when most species utter calls that are difficult to locate (Armstrong 1963:13). Sympatric shorebirds, including the Long-billed Curlew (*Numenius americanus*), Wilson's Phalarope (*Phalaropus tricolor*), Killdeer (*Charadrius vociferus*), American Avocet (*Recurvirostra americana*), and Black-necked Stilt (*Himantopus mexicanus*) give no audible calls during copulations (pers. obs.). Descriptions of the copulation calls of other tringines (Haverschmidt 1963, for the Black-tailed Godwit [*Limosa limosa*]; Nethersole-Thompson 1951, for the Greenshank [*Tringa nebularia*]; Oring 1968, 1973, for Solitary Sandpiper [*T. solitaria*] and Green Sandpiper [*T. ochropus*]) do not emphasize loudness or locatability. Both *klik* and *dik* possess the characteristics of short time span and wide frequency range which make them easy to locate (Marler 1955), and the male's wing display further increases the pair's conspicuousness. Although Willets are strong and swift fliers, wintering flocks do suffer from predation by raptors (Page and Whitacre 1975). Thus the conspicuous copulation seems at least potentially maladaptive. If so,

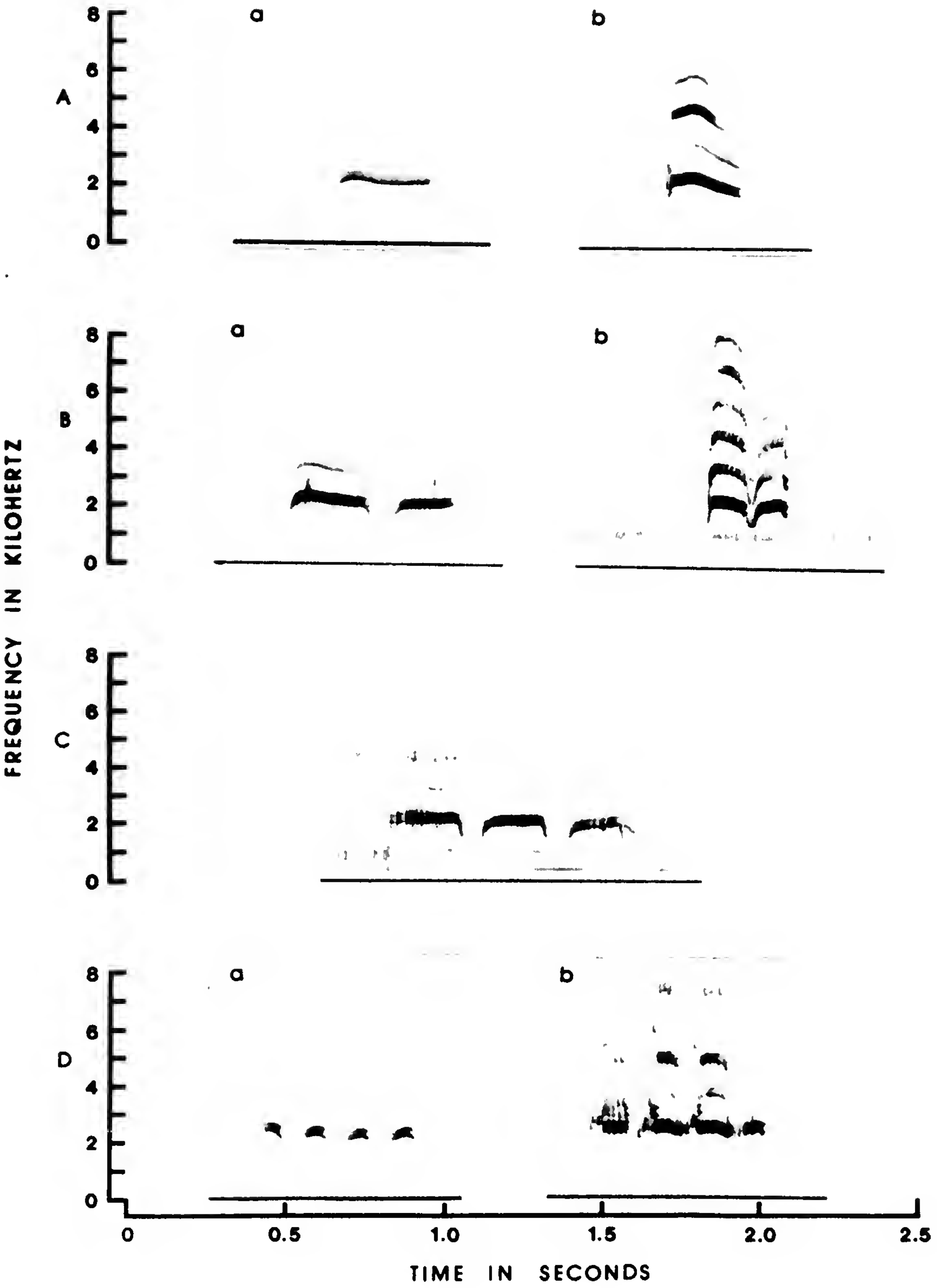

FIG. 3. Spectrograms of Willet *kyah-yah* calls. A. a, b, 2 examples of 1-note variant; B. a, b, 2 examples of 2-note variant; C. 3-note variant; D. a, b, 2 examples of 4-note variant.

counter-selection must be balanced by other selection pressures. What these pressures might be is open to conjecture.

Courtship calls often manifest a mingling of attack, escape, and sexual tendencies (Armstrong 1963:14), i.e., they may represent ritualized agonistic behavior. Both *klik* and *dik* are structurally similar to *kleep* calls, which denote alarm and intolerance. They often grade into *kleep* calls and at times are difficult to distinguish spectrographically. This difficulty is illustrated by the fact that Vogt (1938) described the call given by a male at a border confrontation as what I interpret to be *kleep*, whereas Howe (1974) implicated *klik* in the same situation. Since all other wing displays in Willets seem to contain an aggressive component, I suggest that the entire male copulatory display represents ritualized aggression. Females, when receptive, assume the antithetical appeasement posture with body horizontal and head lowered. When 1 Willet, uttering *klik* calls and wing-waving, approaches another Willet (I usually did not know the sexes of the birds with certainty), the result is either copulation, a chase, or a fight.

Kyah-yah.—This call (Fig. 3) exhibits a great deal of structural variability. It occurs as single- and multiple-note variants, and so I have designated 1-, 2-, 3-, and 4-note variants. It was recorded twice as a 5-note call. Individual notes ranged from 0.07 sec to 0.44 sec in duration, with multiple-noted calls tending to have shorter notes. Second, third, and fourth notes tend to be progressively shorter in duration. They also frequently drop about 0.1 kHz in frequency. Notes are generally of constant frequency but often tail on and off, and sometimes a small inflection is present. A harmonic structure is present with intervals of about 1.1 kHz.

One feature of this call that makes interpretation difficult is the frequent appearance of rapid modulations or frequency displacements of portions of the notes. Virtually any part of any note may be displaced, always upward (higher frequency), up to about 1.0 kHz. Some fragmentation can be seen in the first note in Fig. 3Db. Such modulation might be produced by changing tension in the tympanic membrane, changing pressure in the clavicular air sac, insertion or withdrawal of the external labium in the syringeal passage, or by a combination of these effects (Greenewalt 1968:101). This phenomenon is even more pronounced in the Willet "scream" call, in which it denotes excitement. One is reminded of the cracking of a human voice under stress or excitement.

The variability of *kyah-yah* is expressed in some very different sounding calls. I believe the following (quite aptly named) calls attributed to Willets in the literature are referable to *kyah-yah*: *kiyuk, ki-yi-yuk, kree-uk* (Nichols 1920); *k-a-aty, teee-eeer* (Vogt 1938); *kay-ee* (Peterson 1961); *phwee-hoo* (Tomkins 1965); *whee-wee-wee, whee-hoo* (Palmer 1967).

Possibly with a large sample size some functional subdivision could be made on the basis of structure for this call. *Kyah-yah* is exchanged by 2 or more birds which meet in direct flight. It is given when 1 or more birds fly over other Willets (usually first given by the flying individual and often returned by the bird on the ground, especially when it takes flight to follow). Two or more Willets, or groups of Willets, exchange plaintive *kyah-yah* calls when separated by some distance while feeding or loafing. Birds within large flocks of Willets exchange these calls as if restless, their rate of delivery increasing until the whole flock takes flight amid a volley of multiple-noted variants. During interludes in mobbing, 2 Willets (perhaps members of a pair) often perch on fenceposts and exchange strident 1-note variants.

Thus *kyah-yah* serves as a greeting and contact call, an indication of flight intention, and a flight enticement call which seems important in eliciting a following reaction. A sample of recordings of these calls suggests that an increasing number of notes reflects an increasing motivation to fly. Birds engaged in terrestrial activity gave 1-, 2-, 3-, and 4-note calls in 22, 11, 5, and 0 instances, respectively. Birds engaged in aerial activity gave them in 0, 10, 19, and 6 instances. The difference is highly significant ($\chi^2 = 36.15$, 3 df, $P < 0.001$). A rigid distinction cannot be made between alarm calls and calls indicating that a bird is taking flight for one reason or another (Armstrong 1963:16). Indeed the 1-note variant of *kyah-yah* often seems to communicate a sense of uneasiness among the birds. And the calls given in the mobbing context described above are likely to have an alarm component. One-note *kyah-yah* calls of Willets are structurally similar to 1-note *wheet* calls of the Long-billed Curlew, which signify anxiety and alarm (Forsythe 1970).

Kleep.—This is a double-noted call (Fig. 4), rising slightly on the first note and falling on the second. Its harmonic components span a broad frequency range, with the fundamental sometimes being suppressed. The amplitude and length of notes are variable, which accounts for the variety of descriptions in the literature: *wek, kerwek, piuk* (Bent 1929); *dik* (Vogt 1938); *kip* (Peterson 1961); *kleep, klip* (Tomkins 1965).

Kleep is one of the most frequently heard calls during the breeding season, especially during the incubation and fledgling care periods. The fact that it was already being given when Willets arrived in the spring has led me to speculate that it may occur year-round (Table 1). However, it is probably rare outside of and may be restricted to the breeding season as is the similar *ki-keck* call of the Long-billed Curlew (Forsythe 1970).

Bent (1929) called this the "usual note" of the Willet, which testifies to the conspicuous behavior of the bird as it *kleeps*. It is given by birds which are obviously disturbed (other activities are ceased and an alert posture is assumed), and is used in mobbing. The call is vehement, piercing, and

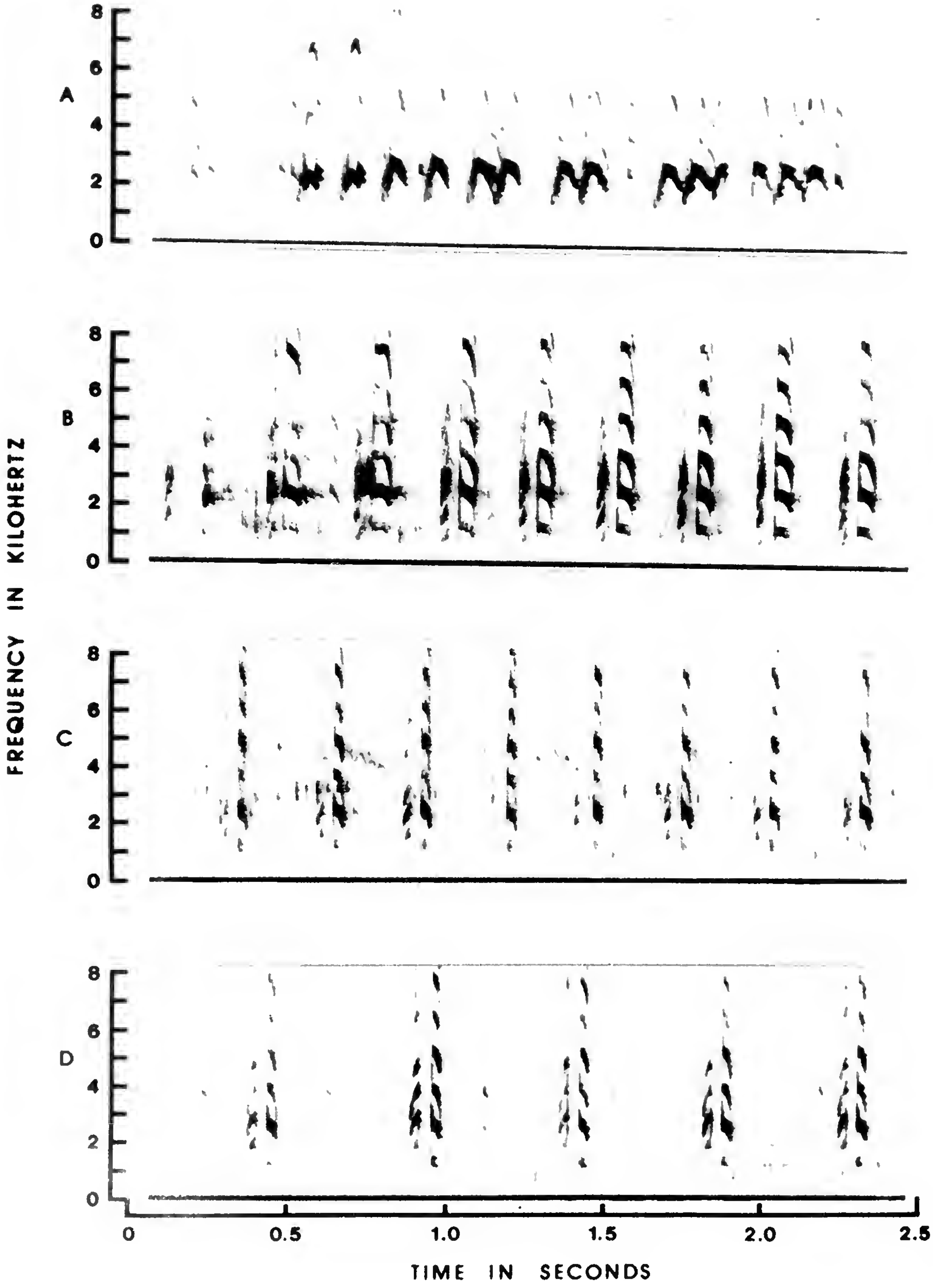

FIG. 4. Spectrograms of Long-billed Curlew and Willet vocalizations. A. Long-billed Curlew *ki-keck* call (1-, 2-, and 3-note variants); B. Willet high intensity *kleep* call; C. Willet medium intensity *kleep* call; D. Willet low intensity *kleep* call.

incessant. With brief pauses it may be repeated by mobbing birds for over an hour. Mobbing, as practiced by Willets, is a very noisy event. In its most intense form it consists of what Hamilton (1975) has called "dive-bombing displays" for American Avocets and Black-necked Stilts. As noted by Tomkins (1965:161), however, there is little actual physical contact involved when Willets mob. This may be related to the fact that shorebirds have sensitive bills (Willets and 8 other species I have handled usually avoided bill contact and almost never bit or pecked at me), but their bluffing is impressive. Only once, when a few feathers drifted down from the back of a Marsh Hawk (*Circus cyaneus*), was I certain that a Willet had made contact.

Willets have been said to "call from a calling post" (Forsythe 1970) and to "bob their heads when walking or standing" (Palmer 1967). Both activities are associated almost exclusively with *kleep* calls and a state of alarm. It is not uncommon for temperate-latitude scolopacids to perch on poles, wires, or in trees (pers. obs.). Head-bobbing consists of a violent backward jerking of the head while keeping the bill parallel to the ground. This is an anxiety movement typical of many species of Charadrii (Maclean 1967, pers. obs.). Apparently the behavior of the Willets, as well as the structure of their calls, is designed to attract attention.

Many species of birds reveal degrees of alarm or the imminence of danger by varying the loudness or rapidity of their calls (Armstrong 1963:17). This is true on both counts for Willet *kleep* calls. Following this idea I arbitrarily divided *kleep* into 3 categories based on calling rate (Table 2). A sample of recordings suggests that these categories do represent high (interval between calls $< 2 \times$ duration of calls), medium (interval between calls 2–3 × duration of calls),and low (interval between calls $> 3 \times$ duration of calls) intensity alarm responses. Birds engaged in terrestrial activity gave the high, medium, and low responses in 3, 11, and 10 instances, respectively. Birds engaged in aerial activity gave them in 11, 6, and 1 instances. The difference is significant ($\chi^2 = 12.81$, 2 df, $0.001 < P < 0.005$). Aerial activity is equivalent to active mobbing and dive-bombing, and is thus a higher-level response. Two of the 3 birds giving high intensity *kleep* calls terrestrially were also head-bobbing vigorously from fenceposts and took flight shortly after. In other studies, too, calling rate has been associated with flight motivation (Andrew 1961) and mobbing intensity (Cully and Ligon 1976).

The following potential predators of Willets, their eggs, or young have been observed to elicit mobbing from Willets on my study area: humans, dogs, striped skunks (*Mephitis mephitis*), California Gulls (*Larus californicus*), Ring-billed Gulls (*L. delawarensis*), Marsh Hawks, Swainson's Hawks (*Buteo swainsoni*), Short-eared Owls (*Asio flammeus*), Black-billed

Magpies (*Pica pica*), Common Crows (*Corvus brachyrhynchos*), and Common Ravens (*C. corax*). Other predators I saw in the area were Great Horned Owl (*Bubo virginianus*), long-tailed weasel (*Mustela frenata*), red fox (*Vulpes fulva*), and common garter snake (*Thamnophis sirtalis*).

Mobbing is an important activity during the fledgling care period. In 1975 I first noted mobbing behavior on 12 May and saw it last on 10 July. The parents stand like sentinels, with the chicks usually somewhere between them. One pair, escorting chicks on the afternoon of 23 June 1975, averaged 4 chases per h of gulls and hawks (observation time = 3 h). A few observations of Common Crows and Black-billed Magpies taking great interest in the locations from which mobbing Willets flew up suggest that some predators may learn to key on mobbing behavior.

Both Vogt (1938) and Tomkins (1965) noted that Willets mob in groups. This is facilitated by the breakdown of territorial boundaries after hatching (Tomkins 1965:160). I saw little hostility between Willets at this time. Ten or more adults may participate in mobbing, with recruits sometimes coming from a considerable distance.

Though it seemed that only breeding birds mobbed actively, apparent nonbreeders and even fledged juveniles were sometimes attracted to mobbing scenes. They would fly in wide circles or land and walk about in the grass. Though Willets are said not to have a distraction display after hatching (Tomkins 1941), I often became confused as to which gray bird running through the grass was the fledgling, and I suggest that the very presence of all those birds constitutes an effective diversionary display (*sensu* Armstrong 1949).

Long-billed Curlews often join these mobbing groups. In my notes I recorded 8 observations of Willets joining other Willets and 5 observations of curlews joining Willets. In addition I recorded 3 instances of Willets joining curlews and 2 instances of curlews joining other curlews. Rarely, other species such as American Avocets, Black-necked Stilts, and Red-winged Blackbirds (*Agelaius phoeniceus*) participate. Both the breeding ranges (A.O.U. 1957) and habitats (pers. obs.) of Willets and Long-billed Curlews overlap broadly. Thus adults and especially their eggs and young are endangered by the same predators. It would be adaptive for individuals of either species to respond to the mobbing activities of other birds as well as to the predators themselves (secondary and primary responses, respectively, of Altmann 1956). This would (1) keep them apprised of the whereabouts of predators in the area, and (2) drive those predators out of the area. Group mobbing by Willets and Long-billed Curlews has been noted independently by D. M. Forsythe (pers. comm.) and myself in northern Utah, and by R. S. Sharpe and T. K. Bicak (pers. comm.) in western Nebraska.

The curlew *ki-keck* call shares a structural similarity with the Willet *kleep* call (Fig. 4A,B). Both calls are loud, have a sudden onset, and cover a broad frequency spectrum, and are thus easy to locate (Marler 1955). Resemblances of this kind have been interpreted as an example of evolutionary convergence in the mobbing calls of passerines (Marler 1959). It is unclear whether *kleep* and *ki-keck* have converged or reflect phylogenetic affinities. Furthermore, it is uncertain whether the observed interspecific responses result from auditory cues or visual ones, as the form of mobbing displays in the species is also similar. However, I believe the most reasonable hypothesis is that vocalizations attract attention to a general area and visual cues reveal the bird's precise location. Whether the responses are learned or built-in might be elucidated by further observations and playback experiments on allopatric populations.

"*Scream.*"—This call (Fig. 5Ab,B,C) is quite variable, especially in note duration. It comprises a single note which begins and ends gradually, and consists of a relatively narrow frequency band. Sometimes harmonic elements appear. But most striking is the rapid and irregular (and unpredictable) frequency modulation which breaks it into a multiple-note call. This phenomenon was discussed earlier for the *kyah-yah* call. The form of the call is remarkably similar to a basso *eeee* or chick distress call (compare Fig. 5, C and D). This similarity, along with the contexts in which it is given, suggests that "scream" may be derived from *eeee*. This is compatible with evidence that in a number of species (including the Eurasian Curlew [*Numenius arquatus*]) the vocabulary of calls has expanded from the calls of the chicks (Armstrong 1963:18). Forsythe (1970) thought that the *pert* call of Long-billed Curlew embryo-chicks developed into the adult *ki-keck* call. It is apparent in some "scream" calls that the Willets were employing 2 separate sound sources (overlapping notes of unrelated frequencies are present).

The situations in which "scream" is given indicate that it reflects a high degree of excitement. Twice Willets uttered these calls as I seized them. Many birds give similar calls in this context (Armstrong 1963:17), and they are likely to be effective in startling a predator into loosening its grip. I have arbitrarily divided this call into 2 categories, based on the apparent motivation of the calling bird. "Scream" attack occurred in such situations as when a pair of Willets mobbed a Short-eared Owl on 12 May 1975 (Fig. 5Ab); when 5 Willets, 2 Long-billed Curlews, and a Red-winged Blackbird mobbed a Marsh Hawk on 22 June 1975; and when 1 Willet mobbed a flock of Common Crows on 10 July 1975. "Scream" flee was recorded when a Willet was attacked by a territorial male Red-winged Blackbird on 14 April 1975 (Fig. 5B); when a long-tailed weasel nearly captured a Willet on 12 May 1975; and several times when I apparently startled Willets into flight. These 2 types of "scream" calls (Table 2) are separable on the basis of call duration ($t = 7.33$, $P < 0.001$) but not by interval between calls ($t = 0.63$, NS) or average frequency ($t = 1.92$, NS).

One reason for the shorter duration of "scream" attack calls is that they often grade into *kleep* calls during mobbing. "Scream" attack and *kleep* calls have the same average emphasized frequency ($t = 0.61$, NS) and similar intervals between calls ($t = 2.04$, $0.01 < P < 0.05$), but differ in call duration ($t = 5.39$, $P < 0.001$). Tomkins (1965) mentioned that *kleep* sometimes approaches a scream. There are probably elements of aggression and distress in both "scream" attack and "scream" flee. "Scream" seems, more than anything else, to be a quality of voice which is related to extreme excitement.

Cluck.—This call (Fig. 2Da,b) is a staccato series of notes which is quite variable in all temporal components. It is given in social contexts which indicate that its major function is that of a distance increaser. For example, birds *cluck* as they feed or move about among other Willets. Observations on flocks showed that it is given by individuals that appear annoyed by conspecifics, and that it causes those conspecifics to move away slightly. Frequently it is accompanied by a flap-and-hop display or a wing-up display, both of which serve to clear more space for an individual in a dense flock. American Avocets and Black-necked Stilts also employ a flap-and-hop display when feeding in tight flocks if neighbors approach too closely (Hamilton 1975:32).

Cluck is a subdued sound, inaudible beyond about 25 m. Consequently it is difficult to obtain good recordings without putting the entire flock to flight. But when minor altercations occur within flocks, the calls become louder as they grade into *kleep* calls. This supports the contention that *cluck* has both aggressive and alarm components. One gets the impression that a Willet is muttering *kleep* calls. For *cluck* also the calling rate seems to be directly related to the proximity of conspecifics and the degree to which the bird is agitated.

Hunker-hunk.—This call (Fig. 2Ca,b) is unusual in that it may not have communication value, although the possibility that *kleep* and *pill-will-willet* calls given by conspecifics were responses to it cannot be excluded. It is clearly composed of a series of fragments of the *pill-will-willet* call. These fragments are highly variable in structure and may occur in a different sequence than they would in *pill-will-willet* (Fig. 2Cb). The series of fragments or note clusters contain from 2 to 5 notes ($\bar{x} = 3.00$, SD $= 1.10$, N $= 6$). Birds may give the *hunker-hunk* call intermittently for 15 min or more.

Hunker-hunk is a moderately loud call, but does not seem to be directed toward other birds. Rather, it seems to be an expression of conflicting tendencies within the bird. It is heard most often during the pre-nesting and incubation periods, when Willets are strongly motivated to give aerial displays. It is probably rare, if it occurs at all, in the nonbreeding season.

A feeding Willet frequently gives this call when a neighbor begins an aerial display, thereby revealing an inclination to join the performance. The opposing urge usually seems to be feeding. Depending on which is more compelling at the moment, a Willet either walks along feeding, occasionally raising its head to utter *hunker-hunk* calls, or launches into the air calling *pill-will-willet.* Willets landing to feed after lengthy aerial displays sometimes give this call, and after a period of feeding, they often give a few *hunker-hunk* calls before beginning the next aerial display.

"*Warble.*"—This call was heard only 3 times, and I was unable to record it. On 21 June 1975 at 18:30 I watched 2 adult Willets and 1 downy chick feeding in a wet pasture. For about 30 min the adults fed toward me, always about 40 m apart and with the chick always between them. When they were about 20 or 30 m from me, I heard 1 adult give a rapid "warble." The call was repeated twice in the next few minutes. After the first call, I noticed that the chick had crouched. The next time I heard the call I saw that the chick was up and feeding again. The call was given again, and the chick crouched again, as I walked into the field (thus making it impossible to ascertain whether it was the call or the observer that caused the chick to crouch).

On each of the 3 observations of "warble," it graded into 1 or 2 terrestrial *pill-will-willet* calls. Spectrographic analysis might show that it is referable to *hunker-hunk* (which it resembled, to my ear), but I have considered it a distinct call because of its apparent function in warning the young.

"*Whistle.*"—This call, shown in Fig. 5Aa among *kleep* calls of an adult which was mobbing me, is a high-pitched 2-noted whistle. It was recorded only twice. On 2 July 1974, at 19:00 as I restrained a downy chick, 1 adult was persistent in mobbing me. One other Willet, which I identified as a juvenile, circled overhead as though mobbing, but remained silent except for a few "whistle" calls. This continued for about 30 min, and I recorded about 15 "whistle" calls. On 2 July 1977, 2 fledged juveniles (with no attending adults) exchanged a few of these calls as I observed them from approximately their normal flight distance. Thus "whistle" may function as a contact or alarm call for juveniles.

Eeee.—This call (Fig. 5D) is given only by young in the preflight stage. Its structure is such that it attenuates rapidly and is difficult to locate (Marler 1955). I heard it only from chicks that were in imminent danger (from me). A chick trapped in the open ran until it was about to be caught, then resorted to *eeee* calls. When held in the hand, chicks always gave

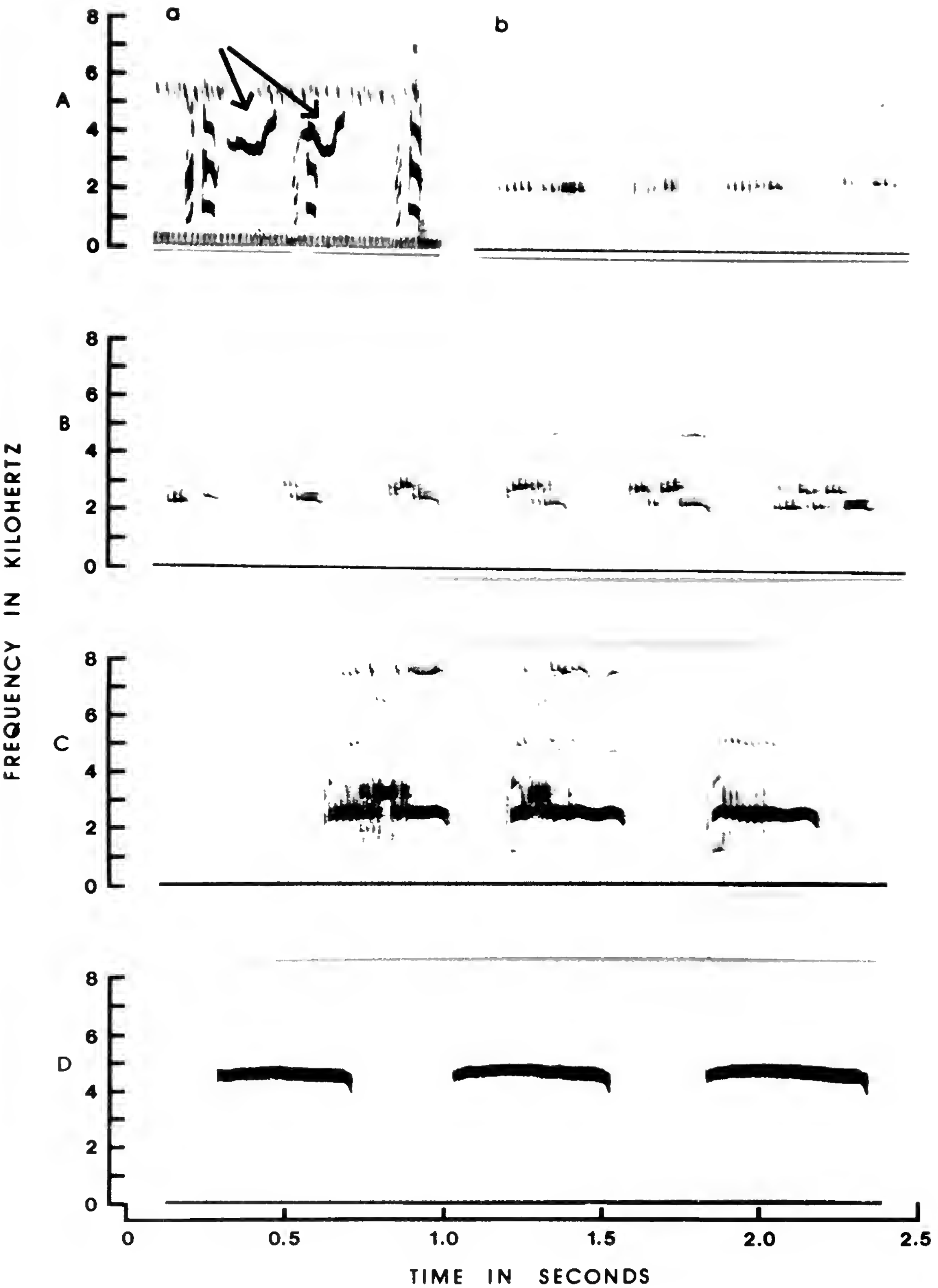

FIG. 5. Spectrograms of Willet vocalizations. A. a. "whistle" call and b. "scream" attack; B. C. 2 examples of "scream" flee; D. *eeee* call.

this call. On 21 June 1975, I watched a chick feeding and mentally marked the spot where it crouched as I approached. Its camouflage was so good that it took me over 10 min to locate it on the open field. Not until I held it high off the ground did it begin to squirm and utter *eeee* calls. When I released chicks, they usually became silent as they ran into the grass. Thus chicks devote their energies to escape until they are actually or very nearly caught. Their major means of escaping predators is hiding at the first alarm of the watchful adults, and then relying on the adults' mobbing and diversionary tactics.

The effect of *eeee* calls on adults is to heighten their level of excitement. *Kleep* calls become more intense, "scream" calls more frequent, and dive-bombing more vigorous.

Tomkins (1965) thought that the "thin wiry call" of young chicks served to keep the brood together and to keep the adults apprised of their location. The poor locatability of *eeee* calls makes me skeptical about such a function. In my experience *eeee* serves as a distress call which seems to elicit harassment of intruders from other Willets.

DISCUSSION

I have recognized 10 adult vocalizations and 1 chick vocalization for the Willet. Previous verbal descriptions have included 10 adult (Vogt 1938) and 1 chick (Tomkins 1965) vocalizations. However, I am unable to account for 4 of the 10 calls described by Vogt: "*yoicker-yoick*," "compulsion note," "a note that suggested the sound made by ruffling a deck of cards," and "contact note."

At least 4 of the Willet vocalizations identified in this study serve to decrease distance between conspecifics, and at least 4 do not (Table 1). Except for *cluck*, which operates only at close quarters, those not decreasing distance (*pill-will-willet*, "scream," and *hunker-hunk*) are probably rare outside the breeding season in this gregarious species.

Willets have vocalizations corresponding to about 7 of the 12 broad categories for signal function identified by Smith (1969). These are: identification, probability, general set, locomotion, attack, escape, and copulation. If flight enticement (*kyah-yah*) can sometimes be considered play initiation, the social play category would also be represented. The frustration category may be expressed by a number of vocalizations, but along with the nonagonistic subset, association, and bond-limited subset categories, it is probably conveyed largely by visual means.

Willets have vocalizations which correspond to at least 6 of the 10 functional categories listed by Thorpe (1961:17). That is, they have calls that I consider to be distress calls, territorial-defense calls, flight calls, flock calls, aggressive calls, and general alarm calls. I did not distinguish any specialized alarm calls, pleasure calls, food-finding calls (Thorpe 1961:24), or nest calls. But Vogt (1938) described a call that may be a nest call.

Where communication purposes are adequately served, acoustic signaling should be favored over visual signaling because it is energetically more efficient (Wilson 1975:236). But open habitats are a difficult environment for sound propagation, due largely to wind-speed and temperature stratification. These conditions diffract the sound wave-front upward, producing a soundless area or "shadow zone" effect which can be erased if a bird calls from as little as 3 to 7 m above the ground (Morton 1975). Willets perform their song-flights at a minimum of 10 m, thus increasing their broadcasting effectiveness. This, along with the need for a better view, may also help account for the tendency of Willets to use elevated perches for sounding alarm (*kleep*) calls. Song-flight is a nearly universal characteristic of tundra and open country birds (Armstrong 1963:221).

Morton (1975) predicted that open country birds should not base information transfer on sound frequency (which is easily distorted by the abovementioned environmental conditions). Instead he suggested that information coding should be based on temporal components, which remain little affected as long as the sound is audible. The length and spacing of notes of the Willet are more variable than their frequency. Most Willet vocalizations have emphasized frequencies of about 1.5 to 2.5 kHz, and therefore a relatively low attenuation rate. Only "whistle" and, to a lesser extent, *pill-will-willet* exhibit any appreciable frequency changes. The signal content of both *kyah-yah* and *kleep* has been shown to vary on the basis of temporal differences. And *klik*, *dik*, *cluck*, and *kleep* seem to be related structurally, but have marked temporal differences.

A refinement of Morton's interpretations (Marten and Marler 1977; Marten et al. 1977) generated similar predictions relevant to the maximization of sound transmission by Willets. The birds should: (1) vocalize from more than 1 m above the ground; (2) use low frequency sounds of approximately 2 kHz; and (3) produce loud sounds with the energy concentrated in a relatively narrow frequency band. These predictions are upheld. Thus both the behavior of Willets and the structure of their vocalizations show evidence of having evolved under the selection pressures of an open country habitat.

SUMMARY

Free-living Willets were studied during the breeding seasons of 1974 and 1975 in Cache County, Utah. A spectrographic analysis is presented for the 1 chick and 10 adult vocalizations recognized in this study, and a numerical and a biological description is given for each call. The song-flight, copulatory behavior, and antipredator behavior are discussed.

The vocal repertoire of the Willet is discussed in terms of its adaptiveness in an open

country habitat. It is suggested that the information of Willet sound signals is encoded primarily in temporal rather than frequency components.

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SOME ASPECTS OF THE BREEDING BIOLOGY AND BEHAVIOR OF THE GREAT BLACK-BACKED GULL

Nicolaas A. M. Verbeek

Three species of gulls nest on Walney Island, Cumbria, England: Herring (*Larus argentatus*), Lesser Black-backed (*L. fuscus*), and Great Black-backed (*L. marinus*) gulls. The last-named species has received little attention. Although my main research dealt with Herring and Lesser Black-backed gulls, whenever time permitted I studied the Great Black-backed Gulls. My main objective was to provide baseline information on the small but expanding population of this species on the island.

METHODS

Observations were made between 4 March and 5 August 1973, and 4 March and 31 July 1974. Behavioral observations were made from 2 portable blinds, each located near clusters of nests. Nests were visited irregularly; at times daily, sometimes not for 2 or 3 days. During each visit records were kept of the nest contents. Food from the nestlings was obtained by sticking my finger in their gullets and extracting the contents. This method was used in 1973. No food was obtained from the nestlings in 1974, though food items found within 1 m of the center of the nests were collected. To determine the influence of the tides on the foraging rhythm of adults, I counted from the blinds all the Great Black-backed Gulls I could see on their territories at 30-min intervals. These counts were made only in the period prior to egg-laying.

RESULTS AND DISCUSSION

Nests.—The Great Black-backed Gulls nested around the ponds resulting from dredging for gravel (Fig. 1). Most nests (31) were placed on slightly elevated positions on gravel piles and ridges; others (19) were placed on flat grassy or sandy soil. Heaps or flat areas with large stones were especially preferred. The nests were placed close to the edge of the ponds. The mean distance from the water edge of 51 nests was 4.94 m (SD = 2.82, range = 1.21–12.19 m). Only 2 nests were located further from the water (39.32 and 45.72 m). Including these 2 nests, the mean distance from the water of all 53 nests was 6.36 m (SD = 7.70).

Although several pairs nested isolated from the others, clusters of nests were apparent (Fig. 1). The mean distance between nests (N = 37) in such clusters was 21.62 m (SD = 10.31, range = 6.10–49.68 m). Nesting close together appeared to be more a matter of choice than a shortage of nesting sites. It appeared that nest-sites were traditional—most of the nests (N = 21) in 1974 were placed in exactly the same position or within 4 m of the 1973 locations.

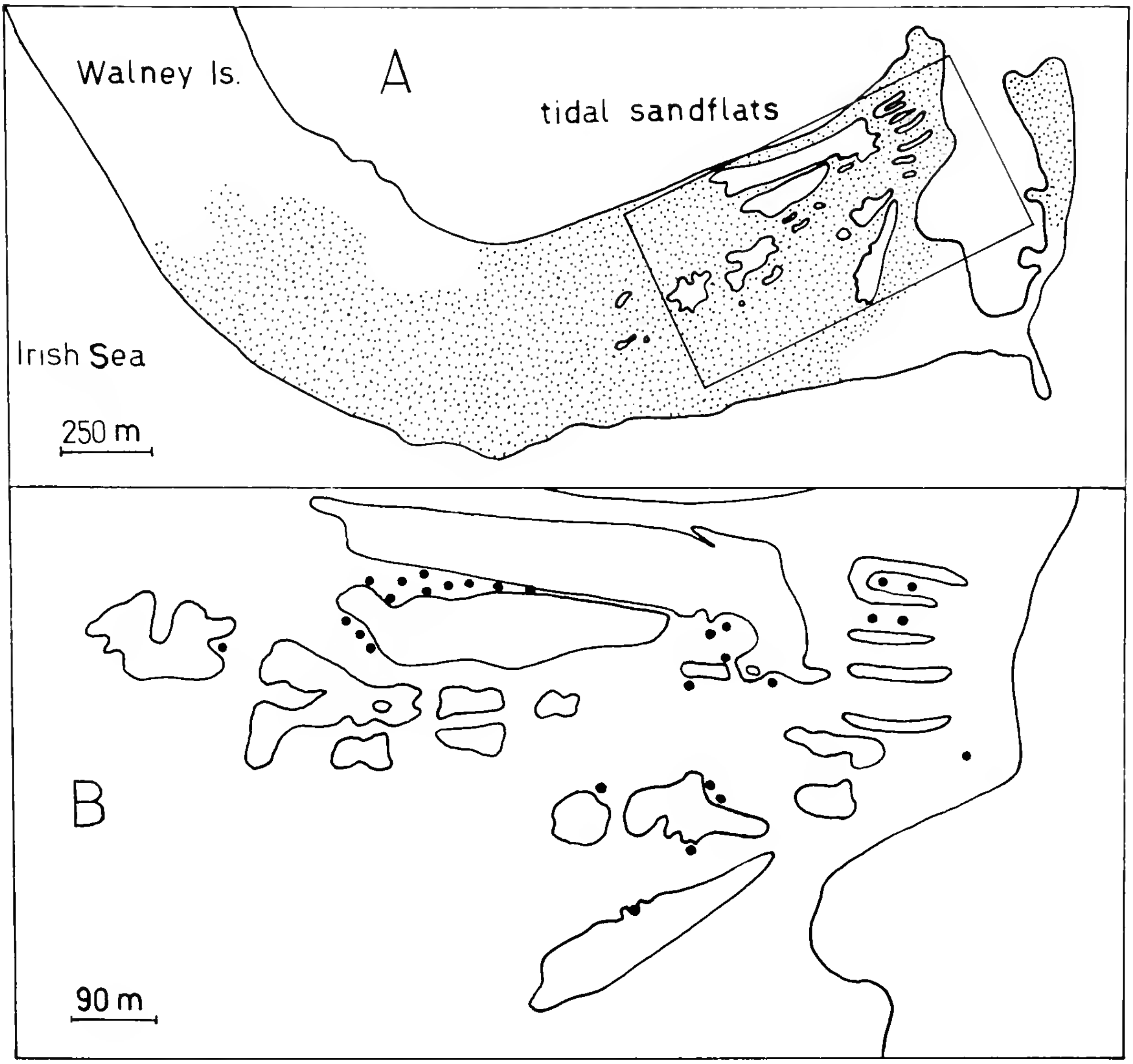

FIG. 1. A. The south end of Walney Island, Cumbria. The stippled area indicates the nesting distribution of Herring Gulls and Lesser Black-backed Gulls. The clear spaces within the rectangle represent ponds. B. An enlarged map of the ponds showing the location of 28 Great Black-backed Gull nests in 1974.

Nest material was collected on or off the territory. Much of it was stolen from the nests of Herring and Lesser Black-backed gulls. Early in the season Herring and Lesser Black-backed gulls set up territories and started to build nests near the Great Black-backed Gulls. However, as the season progressed a large clear space developed around each Great Black-backed Gull nest. This resulted from hostility shown by the Great Black-backed Gulls towards the other 2 species, i.e., the continuous depredations on their nest material, or the complete take-over of their nests.

Breeding success.—In recent times Great Black-backed Gulls have nested on Walney Island since 1952 (1 pair, Barnes, cited in Davis 1958). By 1957, 2 pairs nested on the island. This number had increased to 28

TABLE 1

SUMMARY OF GREAT BLACK-BACKED GULL BREEDING DATA

	1973		1974	
	Number	Percent	Number	Percent
Nests[1]	28		28	
Eggs laid	75	100.00	82	100.00
Eggs per nest	2.68		2.92	
Eggs hatched	41	54.67	32	39.02
Eggs hatched per nest	1.46		1.41	
Eggs not hatched	12	16.00	16	19.51
Eggs lost before hatching	22	29.33	34	41.47
Young fledged of egg hatched	17	41.46	19	59.38
Young fledged per nest	0.61		0.68	
Young lost before fledging	24	58.54	13	40.62
Young fledged of eggs laid		12.75		15.58
Percent of successful nests[2]		60.70		39.30

[1] Including all clutches even if not completed.

[2] Nests that produced at least one fledgling.

breeding pairs in 1973 and 1974 (Table 1). This increase is even more spectacular than the population explosion shown by the other 2 gull species on the island (Verbeek 1977).

The first egg was laid in 1973 on 19 April and in 1974 on 20 April. In both years first eggs of Herring and Lesser Black-backed gulls were found about 1 week earlier. On Skomer, Wales, the first egg of Great Black-backed Gulls was laid on 22 April 1962, that of Herring Gulls on 25 April (Harris 1964). On Sandy Point, Rhode Island, Great Black-backed Gulls started to lay eggs 15 days earlier than did Herring Gulls (Erwin 1971). About $^1/_5$ of the eggs failed to hatch (Table 1). In addition, about ⅓ of the eggs were lost prior to hatching. I suspect that in both years some illegal egg collecting was responsible for this, but the main reason for the loss of eggs in 1974 was the death of adults (see below). Three additional nests in 1974 were lost because of gravel dredging operations.

One nest in 1973 contained 1 Herring Gull egg and 1 Great Black-backed Gull egg. These 2 eggs were incubated by Herring Gulls. The egg of the Great Black-backed Gull disappeared prior to hatching; the Herring Gull egg hatched. Two other nests had 2 Herring Gull eggs and 1 Great Black-backed Gull egg each. These eggs were also incubated by Herring Gulls. The eggs of the Great Black-backed Gull did not hatch in either case. One Great Black-backed Gull pair had 2 eggs of their own and 1 egg of either Herring or Lesser Black-backed gulls, which disappeared. These mixed

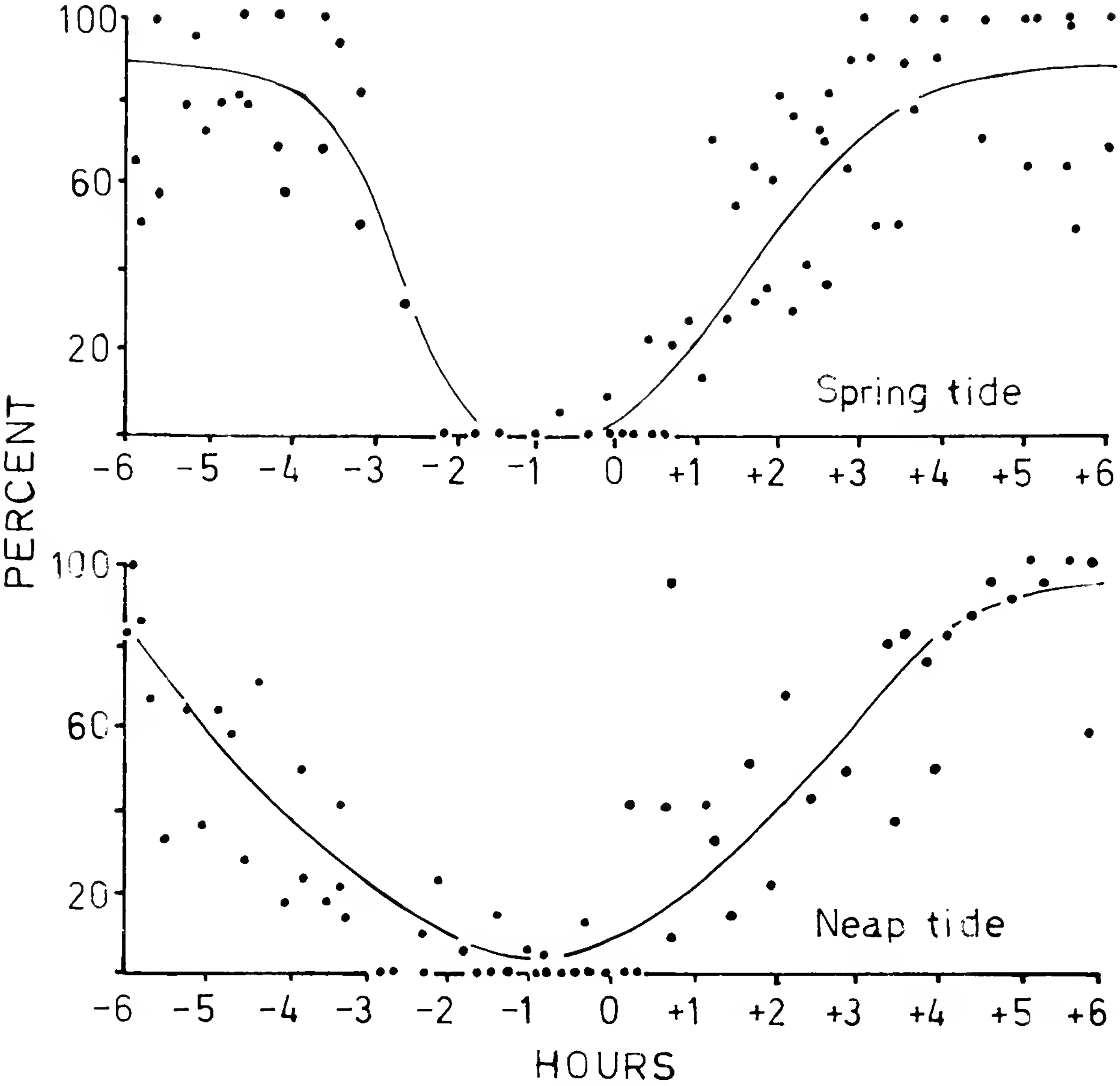

FIG. 2. Percent of Great Black-backed Gulls present on their territories during spring and neap tides. Zero hour indicates the time of extreme low water.

clutches probably resulted because the Great Black-backed Gulls temporarily or permanently usurped the nests of the other species.

Deaths among adult Great Black-backed Gulls occurred in groups. One adult was found on 5 April 1974. Two more adults were found on 6 April; 1 dead, the other incapable of flight; it later recuperated. On 18–19 May 1974, 6 adults were found dead. Two other birds died, both in 1973—an adult on 24 March and an immature bird on 30 March. The latter had broken a wing by flying into a telephone wire. Although no obvious causes of death were found after autopsies, considering that most of the birds died close together (5 and 6 April, 18 and 19 May), I suspect that they might have fed on some poisonous material, perhaps at the nearby garbage dump.

Food and feeding habits.—The foraging rhythm of the Great Black-backed Gull was strongly influenced by the tides (Fig. 2). At low water, both during spring and neap tides, very few or no birds remained in the colony prior to egg-laying. One member of a pair usually indicated its intention to depart for the feeding area by a repeated (once every 10 sec in 1 case) *wok* or *wow* call. Both sexes used the call note for this purpose.

Detailed analyses of the food habits of Great Black-backed Gulls have been made by Davis (1958), Harris (1965), Threlfall (1968), and Kock (1974). In my study, 74 of 133 gullet samples had fish remains, 3 had gull chicks, and 1 had refuse. The other stomachs were apparently empty. In 103 food pellets found around nests, 95 included fish, 22 refuse (mainly bones), 19 crabs, 14 gull chicks (unidentifiable), 8 shellfish, 1 rabbit, 1 Starling (*Sturnus vulgaris*), and 1 land snail. Both Harris (1965) and Threlfall (1968) report large numbers of Manx Shearwaters (*Puffinus puffinus*) and Leach's Petrels (*Oceanodroma leucorhoa*), respectively, being taken. In the absence of other avian prey species on Walney Island, I had expected that the Great Black-backed Gulls would have taken a heavier toll of the Herring and Lesser Black-backed gull chicks. Considering that an estimated 47,000 pairs of these gulls nested on the island, relatively few chicks were taken.

Much of the food of the Great Black-backed Gulls was obtained by stealing it from Herring Gulls and to a lesser degree from Lesser Black-backed Gulls. Many times on the garbage dump I have seen Great Black-backed Gulls merely approach Herring Gulls feeding on some large food item and take it away. I think that on the garbage dump Great Black-backed Gulls fed exclusively by parasitizing the other 2 gull species, especially Herring Gulls. Similarly, in the intertidal regions, Great Black-backed Gulls obtained much of their food by stealing. Even 1-year-old birds displaced adult Herring Gulls with impunity. In the colony, Great Black-backed Gulls often stole food from neighboring Herring Gulls when the latter were engaged in courtship feeding.

Kock (1974) mentions that Great Black-backed Gulls do feed a great deal from commercial fishing vessels, although during 2 days I spent on a trawler on the Irish Sea I saw none among the many gulls attending the vessel when the net was brought up. Several Great Black-backed Gulls were present in the fish harbor at Fleetwood on 30 July 1973.

Behavioral observations.—On 6 occasions I have seen Great Black-backed Gulls flying to where 2 Herring Gulls were locked in combat. At the approach of a Great Black-backed Gull, the Herring Gulls stopped their fight and left. Once, a Herring Gull was briefly chased in the air by a Great Black-backed Gull. On 3 May 1974 an obviously incapacitated Herring Gull flew awkwardly over the colony and was immediately attacked and knocked out of the air by another Herring Gull. As the victim hit the ground a Great Black-backed Gull rushed to the bird and gave it a violent blow on the back with its bill. The Herring Gull managed to fly away and was not pursued.

Among gulls, birds that behave "abnormally" attract the attention of others (Goethe 1939, Tinbergen 1967), and are often treated roughly. For instance, a Herring Gull, entangled in some twine on the Walney Island garbage dump making it fall repeatedly, was viciously attacked by other Herring Gulls. Perhaps then the attraction of Great Black-backed Gulls may be based on this interest in "abnormal" behavior. Secondarily, an abnormally behaving gull may also be an easy source of food.

As stated, Great Black-backed Gulls on Walney Island prefer to nest near water. On several occasions I have seen both sexes, alone or together, gathering nest material and then walking to the water and swimming out on the ponds with the material in their bills. Once on the water, the material is dipped under. In the process of dipping it, some or all of the straws may be lost. On occasion the birds returned with the wet straws and deposited them on the nest. Not all nest material was taken to the water and wetted. I observed the following: between 8 March and 2 April (prior to serious nest building) 5 birds went to the water with nest material and lost it there, 2 birds did not go to the water with their nest material, and none of them deposited nest material on a future nest; between 3 and 14 April, 7 birds took nest material to the water, 2 of them lost it there, and the other 5 placed the wet straw on their nests; 2 birds did not soak their nest material; on 21 April, a 2-year-old Great Black-backed Gull (interscapular feathers just turning black) carried straws in its bill to the water and lost them there. In 5 instances where Herring Gulls were nesting 1–2 m from the edge of the water, these birds did not dip their nest material. One of them deposited a beakful of grass on the edge of the pond, then went into the water to wash its bill, returned to pick up the grass and proceeded to the nest. Wetting nest material may make it stick together better. This may be important considering the Great Black-backed Gull's preference for exposed and therefore windy nest sites.

I have observed 9 cases where individual Herring Gulls have been attracted to Great Black-backed Gulls when the latter were in the preliminary stages of courtship feeding. In 2 of these cases the Herring Gulls merely stood by, apparently looking for spoils. In the other cases the Herring Gulls in question went through various stages of the courtship begging ritual, including "mewing," "head tossing," and "facing away" (Tinbergen 1967). The following are some edited examples taken from my field notes. On 14 April 1973, "a male Great Black-backed Gull lures his mate who follows him while mewing. Next to the female and following her is a 3-year-old Herring Gull who also mews." On 8 March 1973, "a female Great Black-backed Gull lands near her mate and faces away. He mews and walks to the nest-site. She departs and after flying a semi-circle she lands again. He keeps mewing. Then she flies up 5 more times, each time followed by a Herring Gull who lands and departs when the female Great Black-backed Gull does so, and who also faces away from the male when it lands." Lastly, on 13 April 1974, "a female Great Black-backed Gull head-tosses and walks behind a male Great Black-backed Gull who has a large lump of food in his throat but who appears reluctant to feed her. In the meantime a Herring Gull arrives and follows the pair. Three times the Herring Gull is chased away (twice by the male, once by the female). Following each chase the Herring Gull flies a semi-circle and lands again near the pair, which is followed by facing away and head-tossing." These observations pertain to 2 pairs of Great Black-backed Gulls and 2, possibly 3, Herring Gulls, including a 3-year-old bird. I never saw Lesser Black-backed Gulls behave in this manner.

My first impression was that the Herring Gulls were interested in the spoils of courtship feeding. However, only in 2 of the 9 observations did they succeed in obtaining small fragments of the regurgitated food. The effort the Herring Gulls expended and their active participation in the courtship feeding ritual leads me to conclude that these birds were interested primarily in the male Great Black-backed Gull. All the instances here reported occurred in that part of the colony where I found clutches of eggs belonging to Great Black-backed and Herring gulls. Although I did not see any successful raising of Herring Gull chicks by Great Black-backed Gulls, it is possible that this occurs occasionally. Thus I suggest that the Herring Gulls which behaved as described were imprinted on the Great Black-backed Gulls after having been incubated and raised by them. The occurrence of hybrids (Jehl 1960, Andrle 1972) between these species suggests that on occasion mixed pairs are formed. This probably has its origin in the occasional take-over of Herring Gull nests by Great Black-backed Gulls.

SUMMARY

In 1973 and 1974 I studied the nesting success of 28 pairs of Great Black-backed Gulls on Walney Island, Cumbria, England. This represented the entire breeding population of this species on the island. Most of the nests were placed on slightly elevated positions, close to the water's edge. Much of the nest material was robbed from the nests of Herring Gulls and Lesser Black-backed Gulls. Several nests were found containing eggs of Herring Gulls as well as those of Great Black-backed Gulls. This probably resulted from a temporary or permanent take-over of the nests by the Great Black-backed Gulls. Nesting success was low in 1974, mainly because of the deaths of adults. Poison, possibly obtained on a nearby garbage dump, was suspected. Much of the food was obtained intertidally and much of it was stolen, mainly from Herring Gulls. Food samples obtained from the young as well as food remains collected near the nests showed that fishes form the main diet of the young. Behavioral observations of Great Black-backed Gulls interfering in fights among Herring Gulls, and apparent interspecific courtship between Great Black-backed and Herring Gulls are described.

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TERRITORIALITY IN THE PURPLE MARTIN

CHARLES R. BROWN

Studies on the breeding biology of the Purple Martin (*Progne subis*) have defined territory in the martin as one or several rooms of a martin house which the birds defend with decreasing intensity as the breeding season progresses. Allen and Nice (1952:617) state that a male martin selects 1 room of a house and sometimes "part of a house;" and Johnston and Hardy (1962:247, 253) note that territory consists of "one or two" and "more than one" martin house compartment. Olmstead (1955) wrote of a minimum territory of 1 compartment, although he observed that some males may attempt to dominate more than 1 room. Gaunt (1959) mentioned a "pairing territory." However, there have been no detailed, quantitative studies of territoriality in the Purple Martin. From 1968–1977, in Texas, I studied territoriality in martins.

STUDY AREA AND METHODS

My studies were conducted at 2 martin colonies in Sherman, Grayson Co., north-central Texas, Colony A from 1968–1977 and Colony B in 1977. These colonies consisted of both wooden and aluminum martin houses. In 1968–70, Colony A contained a 6-room house; in 1971, a 24-room and a 6-room house; in 1972, a 24-room and a 12-room house; in 1973, a 24-room, a 6-room, and two 12-room houses; in 1974, same as 1973 plus another 24-room house and a 14-room house; in 1975–76, same as 1974 plus another 12-room and a 6-room house; in 1977, two 24-room houses and two 12-room houses. Colony B contained an 18-room, a 12-room, and two 6-room houses.

Resident male martins at the colonies were captured in specially constructed trapping houses, or as nestlings, and marked with colored and painted bands. The number of birds marked varied from year to year, but 30 to 50% were commonly marked. Present capture techniques used for adult martins have rather low yield, and it was impossible to capture all birds in the colonies; the way is clear for development of high-yield techniques. Although Klimkiewicz and Jung (1977) reported a capture technique which they used with success in Maryland, in Texas I have not had great success with their method. Their technique requires certain architectural styles of martin houses and cannot be used widely until eggs are laid, which is too late in the season for complete studies of territoriality. Fortunately, most unmarked individuals could be recognized by plumage characteristics or distinctive behavior. During each year of the study I spent 900–1000 h observing the colony(ies). Arrival dates for all resident martins were recorded, and throughout the season a file was kept on all individuals, indicating the extent of their territories from day to day. Glossy blue-black male Purple Martins were termed "adults" and light-breasted yearling males were termed "subadults."

RESULTS

Territorial data were recorded for all 158 male Purple Martins occupying the study colonies. Extent of territory in martins at Colonies A and B consisted of martin house compartments and the porches adjoining those

TABLE 1
NUMBER OF MALE PURPLE MARTINS AND THEIR MAXIMUM AND MINIMUM TERRITORY SIZES WITH MALES' MONTHS OF ARRIVAL

Month of arrival		Territory size (no. of rooms)															Mean size
		1	2	3	4	5	6	7	8	9	12	14	18	24	30	36	
February	maximum	0	0	0	2	0	6	0	1	0	5	0	0	4	1	0	12.5
	minimum	5	2	8	2	0	1	0	1	0	0	0	0	0	0	0	2.8
March	maximum	4	4	8	9	2	18	0	4	2	10	0	5	2	0	1	7.8
	minimum	15	12	19	10	0	9	1	0	2	0	0	1	0	0	0	3.3
April	maximum	8	6	9	9	0	5	0	2	0	0	1	0	0	0	0	3.5
	minimum	21	8	5	2	0	4	0	0	0	0	0	0	0	0	0	2.1
May	maximum	7	6	8	1	1	2	0	3	1	1	0	0	0	0	0	3.6
	minimum	11	9	6	0	2	1	0	1	0	0	0	0	0	0	0	2.3
Total	maximum	19	16	25	21	3	31	0	10	3	16	1	5	6	1	1	6.5
	minimum	52	31	38	14	2	15	1	2	2	0	0	1	0	0	0	2.6

rooms. Roofs of martin houses were not defended, and no territorial defense was observed away from the martin houses. I distinguished maximum and minimum territories in martins. Maximum territory was the number of rooms a male defended upon his arrival and establishment at the colony. Minimum territory was the number of rooms a male defended at the end of the season, i.e., while he was feeding young.

The number of male Purple Martins that claimed each maximum and minimum territory size, along with the males' months of arrival, are shown in Table 1. Male martins' mean territory sizes also are shown in Table 1. For 48 (30.3%) males the maximum and minimum territory sizes were identical ($\bar{x}$ = 4.1 rooms). Although Finlay (1971) implied that Purple Martins commonly claim only 1 room in Alberta and Rohwer and Niles (1977) apparently assumed the same in their discussion of spring arrival hypotheses, only 20 males (12.6%) defended 1 room as both their maximum and minimum territories. Of males that claimed multi-room maximum territories, 34 (21.5%) claimed only 1 room as their minimum territories. The largest maximum territory defended by a male was 36 rooms for 12 days after his arrival; the largest minimum territory claimed by a male was 18 rooms.

For some males, the progression from maximum to minimum territory was gradual. These males slowly abandoned parts of their maximum territories as the nesting season progressed. At times, males relinquished portions of their maximum territories in response to strong challenges by other males, but generally males seemed to be unaffected by challenges from intruders. In other males, the progression from maximum to minimum territory was abrupt; one day a male vigorously defended his maximum territory, and the following day he inexplicably confined his defense to his minimum territory. In this study I never recorded a male attempting to enlarge his territory after he restricted his activities to his minimum territory. Males seemed to restrict their territories most frequently while feeding young. Male Purple Martins do not actively build nests or incubate, so when these activities are ongoing, males loaf in the colonies extensively and thus are able to easily defend their territories at this time.

Once established in their territories, neighboring males seldom fought or trespassed onto a neighbor's territory. Observations of banded birds indicated that some neighboring males learned to recognize each other and uttered distinct "greeting" vocalizations when they approached each other at the martin house. There even appeared to be a type of "mutual defense" mechanism in neighboring males. On at least 65 occasions, I observed a male that was established on a territory defend a neighbor's territory while that neighbor was absent. In these cases an intruding male appeared in a territory while the owner was away. A neighboring male, apparently recognizing the intruder as foreign, chased the intruder away and then quickly returned to his own territory. In 32 cases when the legitimate owner returned while the neighbor and intruder were fighting, the owner repelled both neighbor and intruder. An intruding male could become established on a territory in a very short time (<10 min), and then fights between the "established" intruder and owner (when the owner returned) could be quite severe and long-lasting (see Brown [1977a]; Purple Martins are capable of inflicting appreciable injury in intraspecific fighting). Nonetheless, mutual territorial defense may promote stability in the colony by keeping intruders away.

Although Allen and Nice (1952) and Johnston and Hardy (1962) indicated that adult male Purple Martins often tolerated, or were less aggressive toward subadult males, I detected no differences in behavior between these 2 age classes. Adult males treated subadults in much the same way as they treated other adults, and I observed vicious fights when subadults intruded into adults' territories. For descriptions of aggressive behavior used in territorial defense see Allen and Nice (1952), Johnston and Hardy (1962) and Brown (1977a).

Although much attention was directed toward males, I also observed territorial behavior in female Purple Martins, though no quantitative data were collected. In many instances territorial defense in females was identical to that of their mates. A female defended the maximum territory while her mate did so, and she restricted her defense to the minimum territory when her mate restricted his defense. No female maintained a minimum territory larger than her mate's minimum territory. But since pair formation in Purple Martins is largely a choice by the female of a territory and attending male, some females briefly held maximum territories that were larger than their eventual mate's maximum territory. In such cases females claimed territories that included more than 1 male. Apparently the females in these instances were still "indecisive" about which male and territory they "wanted."

While no female maintained a larger minimum territory than did her mate, many males claimed larger minimum territories than did their females. A female frequently confined her minimum territory to the nest hole when laying or incubating, while her mate continued to claim several rooms. This disparity in territory size sometimes results in polygyny (Brown 1975).

My studies (unpubl.) of polygyny in Purple Martins show that this mating system is fairly regular in north-central Texas. Preliminary studies suggest that about 20% of males may engage in polygynous relationships during at least the early part of the nesting season, but only about 5% continue as polygynists throughout the entire season. The remaining 15% claim 2 or more females for varying lengths of time while they control their maximum territories, later "releasing" all but 1 female to other males. All but 1 polygynous male have been adults that arrived in February and March; the exception was a May-arriving subadult bird (Brown, unpubl.). Studies on Purple Martin polygyny are continuing and results will be published later.

Once established, females, like males, seldom fought among themselves. Females also displayed mutual defense of neighboring territories. In Purple Martin pairs, the male generally chased away intruding males and the female chased away intruding females, but females were more likely than males to chase away occasionally intruders of the opposite sex. Firmly paired males usually encouraged intruding females.

Table 1 illustrates that males arriving in February and March claimed larger maximum territories than April and May males ($P < 0.05$, Student's t-test), while minimum territory remained the same for all males ($P < 0.05$). All males that arrived in February and March were adults; 21 of 40 (52.5%) April-arriving males were adults; 5 of 30 (16.6%) May-arriving males were adults.

Since I define minimum territory in Purple Martins as the rooms claimed by a male at the end of the breeding season, minimum territory is an indicator of how much of the colony was controlled by the resident male martins (see Table 2). Rooms used by House Sparrows (*Passer domesticus*) and Starlings (*Sturnus vulgaris*) were not included in any male's minimum territory. For 1968–1977, the mean percentage of rooms controlled by male

TABLE 2

TOTAL APARTMENT-ROOMS CONTROLLED BY MALE PURPLE MARTINS, FEBRUARY–JULY

Year	Rooms in colony	No. of males present	Rooms controlled by males	Percent rooms controlled
1968	6	2	5	83.3
1969	6	3	3	50.0
1970	6	2	5	83.3
1971	30	8	24	80.0
1972	36	8	33	91.6
1973	54	17	48	88.8
1974	92	20	70	76.1
1975	110	25	80	72.7
1976	110	33	75	68.2
1977A	72	26	51	70.8
1977B	42	13	35	83.3

martins was 77.1%. No figures were obtained for the remaining rooms not controlled by martins, but most of them were used by sparrows and Starlings.

DISCUSSION

Anyone attempting an analysis of avian territoriality is confronted with a body of literature (e.g., references in Brown 1969, Wilson 1975) in which few, if any, hypotheses to explain territoriality may be found that have attained general acceptance (Nice 1941; Hinde 1956; Tinbergen 1957; Wynne-Edwards 1962; Brown 1964, 1969; McLaren 1972; Wilson 1975; Verner 1977).

The Purple Martin's territory fits Nice's (1941) Type D1 territory—a colonial species restricted to the immediate vicinity of the nest. In martins, the significant aspect of territoriality is the contraction of territories as the nesting season advances. Nice (1941) recognized that such contraction occurs in some species, and suggested a density-limiting function for territoriality. Density-regulation was advocated by Wynne-Edwards (1962), but such group selection has generally been rejected by other contemporary evolutionary biologists (Brown 1964, 1969; Wilson 1975; Verner 1977). I reject density-limitation as a function of territoriality in Purple Martins, but I concede that it may occur as an incidental effect. Density of nesting martins in colonies can be controlled by the size of the established males' maximum and minimum territories (and by the number of apartment-rooms available for occupancy).

Regarding the functions and evolution of territoriality in Purple Martins, I will consider 2 theories of territoriality: McLaren's (1972) view that territoriality has evolved in most species to promote polygyny, and the "super-territory" hypothesis of Brown (1964) and Verner (1977). I favor McLaren's hypothesis to explain territoriality in general, despite the absence of confirming evidence for some species and certain problems of the hypothesis which McLaren admits exist.

McLaren's (1972:203) thesis is that males "with breeding territories are would-be polygynists." But polygyny is kept at a low incidence through competition in populations of evenly matched males with equal sex ratios, despite strong Darwinian sexual selection for polygyny. McLaren notes that it is incorrect to assume that a female, given a choice of sharing a mate or having exclusive use of one, will always opt for the exclusive use of a male. Some males may be inherently superior in attracting mates, and, by mating with one of these polygynous males, a female produces young that also are superior in attracting mates (McLaren 1972:201).

The low incidence of polygyny that I noted in Purple Martins suggests to me that breeding territory has evolved to promote polygyny, as McLaren hypothesizes. This hypothesis is supported by the temporal contraction of martin territories. As the nesting season advances, fewer potential mates are in the population, and males more profitably may restrict their territories and assist their mates in nesting duties. This is confirmed by my observations that males restricted their territories often when the young hatched, which was after most birds in the population had found nesting sites and few additional mates were available. Earlier in the season during nest-building and incubation (in which they do not participate), males are free to compete for more mates. Following McLaren (1972), my unpublished value of 5% polygynous males in martins meets Verner and Willson's (1969) criteria for classifying a species as "normally polygynous."

According to Brown's (1964) and Verner's (1977) super-territory model, male birds that defend territories larger than that needed in terms of resources accrue a selective advantage by preventing conspecifics from breeding. These super-territory holders thus increase their relative genetic contribution to future generations by preventing conspecifics in the same population from contributing any genes (Verner 1977). Furthermore, Verner's super-territory model "predicts that the maximum area should be defended early in the breeding season." Since more individuals attempt to find territories early in the breeding season rather than later, a super-territory holder must maintain his large territory at that time, in order to exclude other males. As the nesting season continues, defense of the territory becomes unimportant, since few males attempt to establish themselves late in the season. This prediction is verified for Purple Martins. In February and March, male martins' maximum territories are much larger than in April and May.

But the super-territory hypothesis for Purple Martins faces difficulties not encountered by McLaren's polygyny model. When Purple Martins nested in woodpecker holes, before European man installed birdhouses, it is probable that many nested singly, or in very small colonies. It seems doubtful that the super-territory would have been adaptive in those primitive circumstances, simply because populations probably were small and scattered and males may not have had opportunities to exclude others. Presently, colonies are large and population density is high in artificial martin houses, and it is possible that the super-territory now could operate. But since there are many nesting cavities in birdhouses available to martins, it is debatable if a super-territory holder really excludes any birds from nesting. Evidence suggests that non-breeding floaters that exist in martin populations move in and replace lost breeders (Brown 1978). But are these floaters excluded from nesting by super-territory holders, or by interspecific competition (Brown 1977b, 1978) from House Sparrows and Starlings? I think the latter possibility is more likely.

On the other hand, the polygyny hypothesis holds for martins that nested in primitive conditions as well as for those nesting in artificial birdhouses. This hypothesis is based on the inherent superiority of some males in attracting mates. We have no records of martin breeding biology prior to the arrival of Europeans in North America, and it is not known if polygyny in martins occurred then. But, following McLaren (1972), if polygyny did not occur then, territoriality was reduced accordingly. In recent times, more nesting cavities in martin houses have allowed the superior males to compete more noticeably (and more successfully?) for mates, and territoriality is expressed.

About 65% of the male Purple Martins in my study defended more than 1 room as their minimum territory. This is curious, because if, at the end of the season, males no longer try to attract additional mates, the defense of more than the nest hole at the end of the season seems energetically wasteful. But multi-room minimum territories may simply be attributed to artificial nesting houses. Perhaps Purple Martins have not completely adapted to the high apartment-room density of birdhouses. Optimal adaptation to birdhouse nesting will consist of a maximum territory of several rooms to facilitate competition for mates, and then a restriction to 1 room when it becomes unprofitable to compete for mates. Also, many males roost in a separate room while their mates are incubating or brooding. Males may defend a minimum territory of more than 1 room to provide themselves with such a sleeping place, although this may be a recent adaptation (in primitive nesting, there were probably few potential roosting holes adjacent to the nest hole).

Since only 12.6% of the males in my study defended a single room throughout the season, it is surprising that Johnston and Hardy (1962:253) found that more than half of their males in Kansas claimed only 1 room. Perhaps Johnston and Hardy confused actual room occupancy with mere male control of rooms. In Texas, while martins never nested in every room in my colonies, most rooms were controlled by either male martins as part of their territories or House Sparrows and Starlings. There have been few "spare" rooms in colonies. The maintenance of minimum territories larger than 1 room assures that colonies cannot have Purple Martins breeding in all the available rooms.

SUMMARY

Territoriality in Purple Martins in north-central Texas was studied at 2 martin colonies. Two types of territory were distinguished: maximum—the number of rooms males claimed upon their arrival at the colony; and minimum—the number of rooms males claimed at the end of the season. Maximum territories were larger than minimum ones; males arriving in February and March claimed larger maximum territories than males that arrived in April and May. Territory in females closely paralleled territory in males. Unpublished studies suggested that polygyny occurred in about 5% of male Purple Martins in Sherman, Texas. Resident male martins controlled about 75% of all available rooms in a martin colony, with House Sparrows and Starlings using the remaining rooms.

It is suggested that territoriality in Purple Martins has evolved to facilitate polygyny. Polygyny remains at a low incidence because competition among evenly matched males in the population overrides strong sexual selection for polygyny. This hypothesis applies to martins that nested in woodpecker holes before man provided birdhouses and to martins presently nesting in martin houses. Polygyny, as a function of territory, is further supported by the temporal contraction of martin territory. As fewer potential mates are available in the later part of the breeding season, males may profitably restrict defense of their territories and assist their mates in feeding young. Territoriality in Purple Martins resembles the "super-territory" model, which postulates that increased territory size in the early part of the nesting season serves to exclude conspecifics from nesting, increasing the territory-holder's relative genetic contribution. But this model is weakened for Purple Martins because it is doubtful that the super-territory holders exclude any conspecifics from breeding. The maintenance of minimum territories larger than 1 room may indicate that Purple Martins have not adapted completely to the high apartment-room density of artificial birdhouses, or may be an adaptation for males' holding a roosting room.

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TEMPORAL VARIATION IN THE SELECTED HABITATS OF A GUILD OF GRASSLAND SPARROWS

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The selected habitats of grassland birds have been the source of much study (Cody 1968; Wiens 1969, 1973, 1974; Whitmore and Hall 1978). Since the structural character of the habitat is important in the selection mechanism (Hildén 1965, Verner 1975), quantification of bird species distribution on numerous habitat variables has often given insight into species specific requirements.

Wiens (1973) suggested that the time of occupancy of territories may have an effect on site selections. Early arriving Grasshopper Sparrows (*Ammodramus savannarum*) occupied habitats structurally different from those of Savannah Sparrows (*Passerculus sandwichensis*). However, the distinctions between initial habitats were lost as bird densities increased. Lacking fitness data he was unable to determine what effect this had on the ecology of the 2 species. His results imply that habitat, at least in his study area, may be limiting and that the species are forced together as their densities increase. One question that might be asked is that if habitat is not abundant and the species do have to coexist in identical, or nearly so, habitats, what effect does change in the structure of the vegetation during territory occupancy have on the community relationships of the species?

In this study I examine the effect of vegetation growth from spring through summer on the selected habitats of 3 grassland sparrows: the Grasshopper, Savannah and Vesper (*Pooecetes gramineus*) sparrows. To my knowledge such temporal variation in selected habitats has not been investigated for birds, as, in the past, most attempts to relate vegetation structural variables to species have been done only during the "peak of the breeding season."

STUDY AREAS AND METHODS

Current surface mine reclamation procedures have, in many eastern states, created tracts of grassland which are not unlike the Great Plains, at least in avifaunal composition. Such tracts are a new resource for birds and in areas such as northern West Virginia species not abundant in the east are common (Whitmore and Hall 1978).

This study was conducted on several recently reclaimed surface mines in Preston County, West Virginia, at an elevation of ca. 640 m. After coal removal the area was regraded, treated with fertilizer and soil stabilizers and planted with a mixture of tall fescue (*Festuca arundinaceae*), red top (*Agrostis alba*), oats (*Avena sativa*), Timothy (*Phelum pratense*), and birds-

TABLE 1

LIST OF VEGETATION STRUCTURE VARIABLES MEASURED WEEKLY ON THE TERRITORIES OF GRASSLAND SPARROWS; STATISTICAL SIGNIFICANCE AS DETERMINED BY ANOVA OF SPECIES AND TIME DIFFERENCES AND DIRECTION OF CHANGE ARE ALSO INDICATED

Variable	Species	Time	Species × time	Direction of change
Percent basal area cover of grass	*[1]	**[2]	NS[3]	–
Percent forb cover	NS	**	NS	+
Percent litter cover	*	**	NS	+
Percent bare-ground cover	NS	**	NS	+
Litter depth (in cm)	*	NS	NS	NC[4]
Forb height (in cm)	NS	**	NS	+
Effective height (in cm)	NS	**	NS	+
Vertical density of grass	*	**	NS	+
Vertical diversity of grass	NS	**	NS	+
Horizontal diversity of grass	NS	**	NS	+
Total grass density	NS	**	NS	+

[1] * = $P < 0.05$.
[2] ** = $P < 0.01$.
[3] NS = not significant.
[4] NC = no change.

foot trefoil (*Lotus corniculatus*). As natural succession begins, other grass species, including orchard grass (*Diactylis glomerata*), poverty grass (*Danthonia spicata*), velvet grass (*Holcus lanatus*) and rye grass (*Lolium perenne*), become established (Staples 1977).

During the first week of May 1977, territories of Grasshopper, Savannah and Vesper sparrows were located by the territory flush technique (Wiens 1969). The center of the territory was marked and served as the starting point for 2 line transects 25 m in length, the directions of which were determined by a random numbers table and a compass. Several vegetation structure variables were measured on each territory weekly for 11 weeks (Table 1). For the most part the territories were occupied throughout the study period and when the study was terminated on 25 July, most of the sites still had birds on them, although intraspecific defense was not nearly as intense as in earlier weeks.

Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA), as well as univariate analysis of variance (ANOVA) were used to analyze these data. Following the procedures of Harner and Whitmore (1977) p-dimensional niche overlap (habitat use) values were calculated for each species pair, as defined on the habitat structural variables, using the density overlap method, an adaptation of DFA. This measure varies between 0 and 100% with 0% being no overlap and 100% being complete overlap.

RESULTS

Territories of the sparrows showed significant differences in 4 vegetation variables throughout the 11 week study period (Table 1): (1) basal area cover of grass, (2) litter cover, (3) litter depth, and (4) vertical grass density. This means that their territories were different from each other in these structural aspects at the time of initial occupancy as well as in late July. The other variables were not different over the entire period.

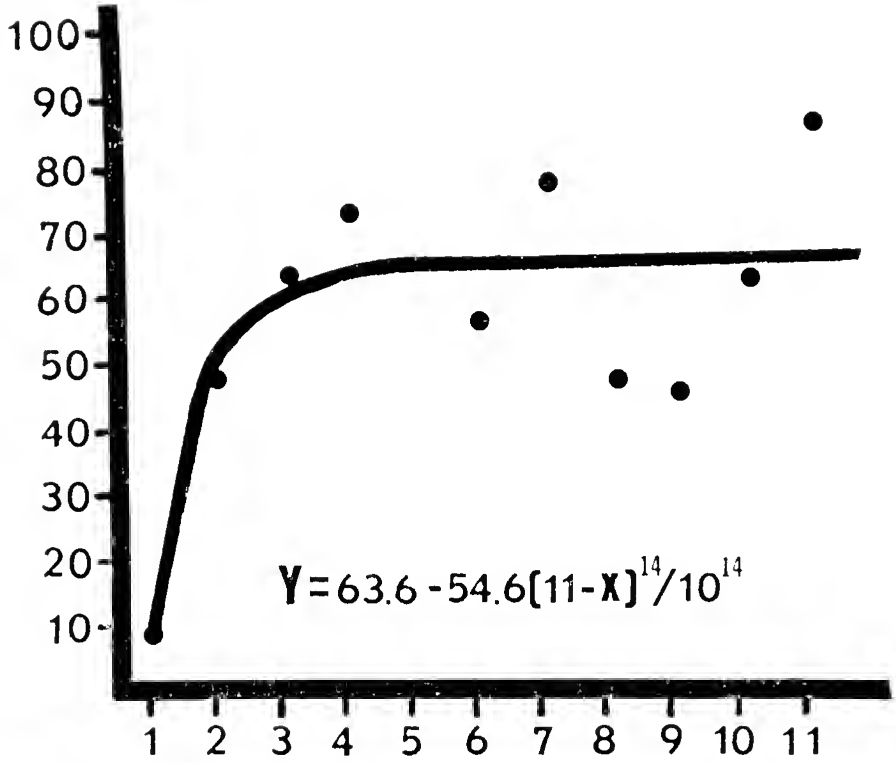

FIG. 1. Habitat use overlaps between Savannah and Grasshopper sparrows plotted over an 11-week period beginning the first week of May 1977. Values are expressed as a percent with 100% representing complete overlap and 0% representing lack of overlap.

All of the variables, except litter depth, did have a significant change with time, while there were no significant species × time interactions (Table 1). Except basal area cover, which has negative changes, and litter depth which did not change, all of the variables had positive changes with time, indicating growth of the vegetation.

When all of the variables were analyzed simultaneously (MANOVA), it was found that there was a significant ($P < 0.01$, $F = 7.28$) change in the habitat over time and that the species were significantly different ($P < 0.01$, $F = 2.48$) from each other in their breeding territories over time. As with all of the univariate interactions, the multivariate time × species interaction was not significant ($F = 1.10$).

The Vesper-Savannah sparrow and Vesper-Grasshopper sparrow pairs did not show any obvious temporal changes in their multivariately determined habitat use overlaps (Table 2). However, in the Grasshopper-Savannah sparrow pair a pattern did emerge (Table 2 and Fig. 1). Habitat use overlap started out to be small, showed a rapid increase and then leveled out. This indicates a distinct separation of habitats early in the breeding season when the birds first arrive. However, by the peak of the breeding season, overlap has increased greatly. A regression line ($r =$

TABLE 2
PAIRWISE MULTIVARIATELY DETERMINED HABITAT USE OVERLAP VALUES BASED ON 11 VEGETATION STRUCTURE VARIABLES MEASURED WEEKLY

Week	Savannah Sparrow Grasshopper Sparrow	Savannah Sparrow Vesper Sparrow	Grasshopper Sparrow Vesper Sparrow
1	9	—	—
2	48	37	62
3	62	68	35
4	72	37	52
5	63	66	28
6	56	36	18
7	76	20	60
8	47	51	42
9	45	31	33
10	63	42	50
11	86	58	42

0.917, $P < 0.01$) can be drawn through the points emphasizing the nature of the change.

Comparing the vegetation of the territories when the birds arrived with that of the peak of breeding activity, shows some interesting relationships. Overall, the territories of each of the species show significant ($P < 0.01$, $F = 6.49$) differences between the 2 periods. This change can be attributed to general differences in percent basal area cover of grass, forb height, vertical density of grass, effective height of vegetation and total grass density (Table 3).

DISCUSSION

Generally, early measurement of territories of the sparrows showed a gradient from open, or sparse grassland with low grass and forb densities, and high bare ground cover to high grass and forb density, and low bare ground cover. Vesper Sparrows occupied areas at the low end of the gradient; Savannah Sparrows were intermediate and Grasshopper Sparrows were at the high end, in the densest vegetation. These relationships were maintained into the breeding season in roughly the same order. The magnitude of difference, as measured by p-dimensional habitat use overlap, remained approximately the same for 2 pairs of species. However, while their positions on the gradient remained the same, Grasshopper and Savannah sparrows showed a marked change in the amount of structure held in common. That is, as the season progressed and the vegetation grew, their territories began to resemble each other, even though the birds hadn't moved. What started out looking like 2 separate habitat types ended up

TABLE 3

VALUES ($\bar{x}$ AND SD) FOR VEGETATION STRUCTURE VARIABLES FOR THE TERRITORIES OF EACH SPARROW SPECIES FOR 2 TIME PERIODS; NEAR ARRIVAL DATE AND DURING THE "PEAK OF BREEDING ACTIVITY"

	Arrival time					
	Vesper Sparrow		Savannah Sparrow		Grasshopper Sparrow	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Percent basal area cover of grass	17.10*	6.98	34.15*	41.37	29.37*	9.74
Percent forb cover	5.54	4.14	7.95	5.30	9.59	6.74
Percent litter cover	53.36	20.64	64.35	6.15	72.91*	18.25
Percent bare-ground cover	44.16	20.64	14.70*	6.65	25.62	17.92
Litter depth (in cm)	1.03	1.15	1.26	1.06	2.07	1.19
Forb height (in cm)	8.13*	5.41	7.93	3.16	6.47*	1.84
Effective height (in cm)	26.25*	5.17	25.00*	7.07	31.00*	7.38
Vertical density of grass	7.62	4.69	9.50	3.54	10.70	3.37
Vertical diversity of grass	0.54*	0.09	0.55*	0.09	0.64*	0.20
Horizontal diversity of grass	0.57	0.31	0.49*	0.11	0.73	0.21
Total grass density	48.50*	27.69	93.50*	3.54	108.60*	40.08

	Breeding peak					
	Vesper Sparrow		Savannah Sparrow		Grasshopper Sparrow	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Percent basal area cover of grass	6.25	9.91	9.35	11.94	5.29	4.61
Percent forb cover	13.77	12.11	12.90	10.34	16.93	13.09
Percent litter cover	56.20	30.61	71.02	19.72	85.97	12.84
Percent bare-ground cover	43.80	30.61	28.58	19.65	13.94	12.88
Litter depth (cm)	1.01	0.57	1.08	0.76	1.51	0.49
Forb height (cm)	13.62	6.39	10.03	4.24	12.88	5.75
Effective height (cm)	53.33	20.61	65.56	16.67	65.45	18.64
Vertical density of grass	9.67	6.52	11.44	4.93	13.45	4.97
Vertical diversity of grass	1.10	0.34	1.31	0.33	1.12	0.33
Horizontal diversity of grass	0.60	0.37	1.03	0.43	0.86	0.24
Total grass density	89.33	51.19	157.44	90.77	169.64	58.52

[1] * indicates that this variable shows a significant ($P < 0.05$) change from week 1 to week 6 for an individual species.

being nearly identical. In fact, Savannah and Grasshopper sparrow territories were significantly different from each other at week 1 (DFA, $P < 0.01$, F = 2.98) but not at week 6 (F = 0.86) or week 11 (F = 0.20).

Wiens (1974) has shown that early arriving Savannah and Grasshopper sparrows select territories that are vegetationally distinct, but that, after the breeding populations stabilized (mid-June), the territories were quite similar. It should be noted that all of his vegetation measurements were made in mid-June. My study does not take into account the time of territory occupancy but does show that vegetation growth can account for statistically significant changes in species specific habitat requirements.

Harner and Whitmore (1977) have shown that the number of variables entered into the model can affect the community patterns obtained. It now appears that the time of measurement can also be a factor affecting these patterns. An investigator measuring bird habitats only during a limited portion of the breeding season could produce results that are strikingly different from those of an investigator collecting data in a period differing by only a few weeks. Moreover, if the vegetation data are collected over an entire breeding season, then some method of factoring out the time effect must be used (Green 1974).

This study also shows that the habitats selected in early spring are for the most part structurally different from those into which the young are fledged after breeding. There is strong evidence that in many bird species, primary emphasis is placed on learning or imprinting during the early nesting state (Klopfer 1963, 1965; Klopfer and Hailman 1965; Hildén 1965; Orians 1971). This could lead one to ask what cues are learned by the fledglings that allow them to select adequate habitats the following spring?

Perhaps those characteristics of the habitat which change radically with time provide little information in the selection of habitats, while those that remain constant, or nearly so, can be learned and remembered when the fledglings come back the following spring. Perhaps a fruitful line of research might be to manipulate certain variables, litter depth for example, that do not show a marked change with time in order to determine their role in habitat selection.

SUMMARY

In order to determine the effect of vegetation growth on bird community patterns, territories of Grasshopper, Vesper and Savannah sparrows breeding on reclaimed surface mines in West Virginia were studied during the summer of 1977. Eleven vegetation structure variables were measured weekly on each territory for 11 weeks during the breeding season. All variables, except litter depth, changed significantly during the study period. Multivariately determined habitat use overlap values showed that Grasshopper and Savannah sparrow habitats, after starting out to be quite distinct, became more similar in structure as the season progressed, going from 9% overlap in May to 86% overlap in July. It was found that habitats for all 3 species measured near the arrival date were statistically different from those measured in mid-June, at the "peak of breeding activity." Therefore, the habitats actually selected differed from those into which the young are fledged.

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HABITAT USE BY NESTING AMERICAN COOTS IN SASKATCHEWAN PARKLANDS

LAWSON G. SUGDEN

American Coots (*Fulica americana*) are the most abundant marsh species using prairie pothole habitat (Stewart and Kantrud 1972), but apart from Kiel's (1955) paper, little has been published on the factors that affect nesting densities and how nesting pairs are distributed throughout such habitat. Discussing research and management needs of the American Coot, Fredrickson (1977) stressed the need to document relationships between populations and habitat. Data for the present paper were collected during a study of Canvasbacks (*Aythya valisineria*) and Redheads (*A. americana*) from 1973–1975.

STUDY AREA AND METHODS

The study area (52°N, 106°W) is a 31.1-km^2 block, 4.83 × 6.44 km, 48 km east of Saskatoon, Saskatchewan. It is divided by roads and fence lines into 12 sections, each 259 ha. The area has been described elsewhere (Sugden 1977, 1978). Pond density averaged 17.6/km^2 in 1973, 23.6/km^2 in 1974, and 26.2/km^2 in 1975; size ranged from <0.04 ha–8.1 ha. Most ponds were partly, or wholly bordered with trees, mainly willows (*Salix* spp.) and trembling aspen (*Populus tremuloides*). The most common emergent species occurring in ponds used by coots were whitetop (*Scolochloa festucacea*), cattail (*Typha latifolia*), and sedge (*Carex atherodes*). *Scirpus* spp. was scarce.

Each year maximum depth of ponds was measured in early May and again in July. Ponds were assigned to 4 permanency categories (Sugden 1977, 1978) similar to those described by Martin et al. (1953) and Evans and Black (1956). Types 1 and 3 ponds are least permanent, whereas types 4 and 5 are most permanent. Pond areas were measured from maps prepared from aerial photographs. For data analysis, ponds were placed in 5 size classes (see Table 2). Ponds were assigned to 3 categories of estimated woody shore growth: open, 0–33%; half-open, 34–66%; and closed, 67–100% (Smith 1971). Land use around ponds was recorded in late May as summer fallow, seeded to grain, seeded to oilseed, or as pasture.

Three coot counts were made on all 12 sections in 1974 during 9–13 May and 4 additional counts were made on 8 sections during 14–23 May. In 1975, 3 counts were made on the 12 sections during 8–15 May. Counts were made in conjunction with duck counts and not all coots were seen. Therefore, assuming the same percentage was seen each time, the results represented an index to numbers of coots present (Kiel 1955:192).

Emergent cover on all ponds was systematically searched twice for nests, the first search commencing in late May and the last ending in late July. The average interval between searches was about 35 days. With few exceptions, only active nests with eggs were recorded. The exceptions involved nests with clutches that had hatched recently or had been destroyed, and when, in the latter case, there was no nest on the pond that could be considered a renest resulting from the one destroyed. Total nests for a given pond were recorded as the largest number found during either search. The maximum number was recorded during the first search on a majority of ponds. In 1974 and 1975, nest locations were plotted on maps, permitting calculation of all new nests, including those that were likely renests based on evidence of destroyed nests.

In 1975, water depth at nest-sites, kind of support, and nest material were recorded. Distances between nests within ponds were also measured in 1975 on all ponds with more than 1 nest on 6 of the sections. To increase sample size for ponds with over 4 nests, such ponds from the remaining 6 sections were included. Nest locations were marked with a stake or a ribbon on a nearby willow. In November, distances between marked nests were measured by pacing between them on the ice and plotting their locations with the aid of a compass.

RESULTS AND DISCUSSION

Excluding type 1 ponds which were not used by nesting coots, the numbers of types 3, 4, and 5 ponds on the block were, respectively, in 1973: 187, 140, 74 (total = 401); 1974: 180, 250, 205 (635); 1975: 248, 279, 174 (701). Proportions of ponds in the 3 categories of woody shore growth were similar in all years and averaged 49% open, 13% half-open, and 38% closed. On the average, large ponds tended to be more open than small ponds ($\chi^2 = 56.2$, df = 8, $P < 0.001$). High water levels prevailed in 1974 and 1975 and much of the peripheral willow growth was inundated throughout those breeding seasons.

Although new nests were found on some ponds during the second search in each year, total nests for such ponds seldom exceeded totals for the first search. In 1973, 410 nests were found on ponds that yielded equal or higher totals during the first search. Thirteen (3.1%) were on ponds that had higher totals during the second search. In 1974, 56 new nests were found during the second search and of these, 26 (4.7%) of the grand total resulted from higher totals for ponds searched a second time. The remaining 30 were probably renests. During the second search in 1975, 159 new nests were found and 52 (5.1%) were on ponds having higher totals during that search. The others (107) were believed to represent renests. In addition to the small proportion of new nests located by second searches, 2 observations helped to justify the method for calculating the total nesting population. Many of the ponds having fewer nests during the first search were among those that were searched earliest (late May). Thus, a pair of coots and perhaps a nest structure would be seen, but the clutch was not present until the second search. On the other hand, when new nests were found but the total for the pond did not increase, there was usually evidence that the original nest(s) had been lost.

Habitat use.—Based on nest counts, there were 423 nesting pairs on the study block in 1973, 555 in 1974, and 1013 in 1975 for respective densities of 13.6, 17.8, and 32.6 pairs/km^2. Nests were not found on type 1 ponds and an average of only 5% occurred on type 3 ponds (Table 1). A similar relationship was shown by Kiel (1955:193) who found only 2.3% of

TABLE 1

COMPARISON OF POND USE BY NESTING COOTS FOR 3 PERMANENCY TYPES AND 3 YEARS

Year	Pond type	Percent of all nests	Percent ponds used	Mean pond area (ha)/nest			
				All ponds	All nest ponds	>1-nest ponds	1-nest ponds
1973	3	7	12	2.11	0.45	0.49	0.42
	4	43	67	0.38	0.32	0.30	0.38
	5	50	80	0.35	0.32	0.30	0.55
	Total	100	44	0.48	0.33	0.31	0.42
1974	3	5	12	1.55	0.36	0.55	0.29
	4	30	46	0.69	0.45	0.49	0.41
	5	65	80	0.54	0.50	0.46	0.61
	Total	100	48	0.63	0.48	0.47	0.49
1975	3	5	19	0.75	0.27	0.29	0.27
	4	35	77	0.32	0.29	0.29	0.28
	5	60	93	0.33	0.33	0.30	0.57
	Total	100	60	0.35	0.31	0.30	0.35
All years	3	5	15	1.32	0.34	0.47	0.31
	4	36	63	0.42	0.33	0.33	0.34
	5	59	85	0.40	0.38	0.35	0.59
	Total	100	52	0.46	0.36	0.34	0.41

the nests on "temporary" ponds, which were roughly equivalent to my type 3. Many of the unused type 3 ponds became dry during the breeding season. Those that were occupied had average nest densities similar to those on types 4 and 5 ponds. A majority of the coots nested on types 4 and 5 ponds in all years. Nest densities on these 2 types (Table 1) were similar. This is contrary to Fredrickson's (1977:125) statement that highest densities occur on type 4 wetlands.

The ability of American Coots to select nest ponds that maintain water throughout the breeding season has been noted by Kiel (1955:194) and Smith (1971:28). In my study, only 2 nests were found on ponds that became dry. Both ponds dried up after the eggs hatched but before the young fledged. The birds may have moved to nearby ponds. The relationship of both pond permanency and size to use by nesting coots in illustrated by mean densities for the 3 years (Table 2). Nest densities on the 12 sections were directly related to the total area of types 4 and 5 ponds. Regression equations for the 3 years are as follows (Y = coot nests, X = ha of types 4 and 5 ponds per 259-ha section): 1973, $Y = 3.23X - 3.61$,

TABLE 2
THREE-YEAR AVERAGES FOR COOT NESTS/POND[a] BY 3 PERMANENCY TYPES AND 5 SIZE CLASSES

	Size class (ha)					
Type	<0.21	0.21–0.40	0.41–0.81	0.82–1.62	>1.62[b]	Average
3	<0.01	0.22	0.55	0.11	1.20	0.17
4	0.45	0.80	1.30	2.29	5.10	1.06
5	0.38	1.01	1.62	3.08	6.92	2.61
Average	0.24	0.67	1.29	2.53	6.28	1.15

[a] Three-year pooled nests/3-year pooled ponds.
[b] Mean size was 2.92 ha.

$r = 0.90$, $P < 0.001$; 1974, $Y = 5.85 + 1.54X$, $r = 0.72$, $P < 0.01$; 1975, $Y = 11.77 + 2.74X$, $r = 0.87$, $P < 0.001$.

Within any of the 5 size classes of ponds, nest densities were unrelated to the amount of tree growth around ponds ($\chi^2 < 5.0$, df = 2, $P > 0.05$). This was also true for the kind of land use around ponds ($\chi^2 = 0.3$, df = 2, $P > 0.80$).

Nesting chronology.—Seven counts on 8 sections during 9–23 May 1974 indicated that the coot population on the area was stable by mid-May. Most, if not all, of the birds apparently nested. Flocks of obviously non-breeding birds were not observed. Notwithstanding the limitations of the coot counts, the low numbers seen compared with the numbers known to nest, also suggested a high incidence of nesting. In 1974, the maximum count yielded but 62% of the number known to nest. In 1975 it was 43%.

Shortage of nesting cover during mid- to late May at the peak of nest initiation, apparently caused some pairs to delay nesting—a phenomenon described for coots in Iowa by Fredrickson (1970:450). Emergent cover became available last on the deepest parts of a few large ponds and the latest nesting occurred here. Some pairs, unable to secure a territory early in the season, did so later when new cover became available. Coots were present on some ponds that lacked cover and nests during the first search (late May); nests were established later when new plants emerged. Fjeldså (1973), in a study of breeding European Coots (*Fulica atra*) on a 140-ha complex of marshes in Denmark, described territorial regulation that involved both space and time. All available nesting areas of the marsh were occupied and egg-laying was underway in mid-April by 1 group of European Coots while non-breeders remained on the open parts of the marsh. As clutches of the first group hatched and the parents with downy young moved into denser cover, pairs from the second group established nests in the vacated territories. The first group comprised 62 pairs and the second group, 40 pairs; the later believed to be mostly first-year breeders, based on nest and egg measurements (Fjeldså 1973:124). In Saskatchewan, the breeding season is at least a month shorter, so is probably too short to allow such protracted use of nesting habitat. Moreover, few marshes would be large enough to accommodate nesting and non-breeding birds simultaneously. Any delayed nesting on my area was caused mainly by late growth of nesting cover, not the vacating of space by early nesting pairs.

Nest distribution.—The distance from 1 nest to the nearest nest within a pond was measured for 577 nests on 121 ponds in 1975. Distances ranged from 22 to 145 m ($\bar{x}$ = 54 ± 20 m). Mean distance did not differ among pond size classes or with numbers of nests per pond ($P > 0.05$, Duncan's new multiple-range test). Only 22% of the nests were closer than 40 m. Some of the closest nests were separated by dense cover, particularly willows and cattails, which would reduce interpair contact (Fjeldså 1973:119). However, a few had no such barriers; these usually occurred on small ponds with the longest axis equal to the nest-to-nest distance.

Gullion (1953:181) showed that the distribution of coot nests on 2 California wetlands, 1.1 and 4.9 ha, was governed mainly by territorial spacing and the distribution of nesting cover. This was also true for the pothole habitat in my study where total amount of emergent nesting cover was unimportant. Small patches of cover (often isolated willow or cattail clumps), well distributed throughout a pond, were used as efficiently by coots for nesting as were extensive stands of cover. Few ponds were without some cover near shore and on many ponds cover occurred only here; nest distribution (Fig. 1) reflected these cover patterns. On large ponds the complete lack of cover in the interior portions probably limited the number of nesting pairs that the pond could otherwise have supported (Fig. 1). However, on large ponds with well-dispersed cover, coots tended to nest farther from shore. Therefore, lack of interior cover would, in part, be compensated for by the relatively high use of peripheral areas dictated by cover distribution. In 1975, 6 ponds over 3 ha with only peripheral cover had a mean density of 2.8 nests/ha compared with 3.7 nests/ha on 4 ponds having well-distributed cover. The difference was not significant ($t = 2.03$, df = 8, $P > 0.05$).

These results cannot be considered conclusive because no 2 ponds were alike in size and shape, both of which interact with cover dispersion. As ponds become smaller and/or depart from a circular shape, lack of interior cover would become less important and be replaced by territorial spacing as the key factor limiting nest densities on ponds having only shore cover. Available space would limit the number of nests regardless of their loca-

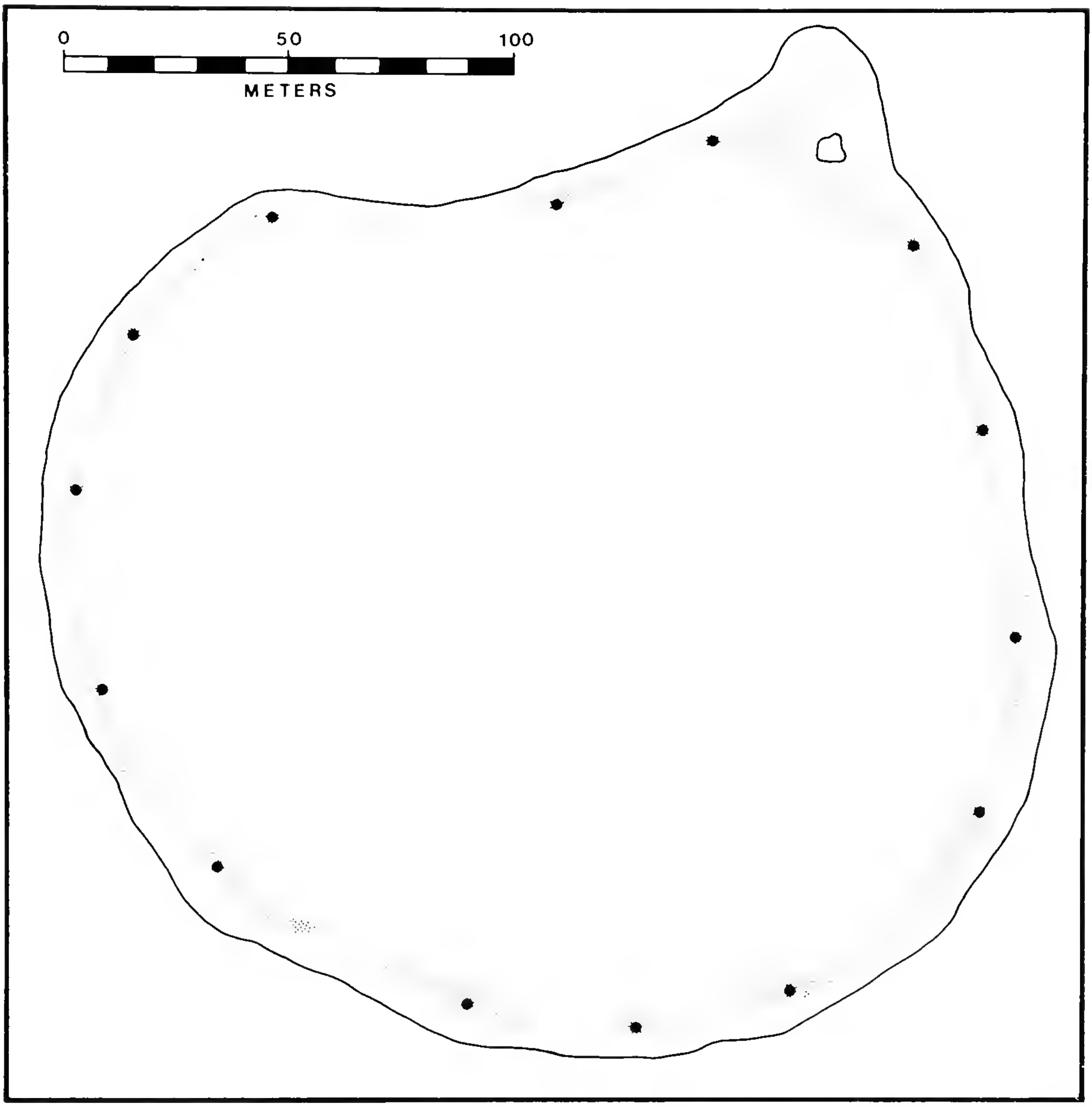

FIG. 1. Distribution of 14 coot nests on a 3.75-ha pond having only peripheral *Scolochloa festucacea* cover (shaded), 2 June 1975.

tions. On many ponds under 2 ha with more than 1 nest, the fact that nesting coots were restricted to shore cover probably permitted higher nesting densities than would have been possible where pairs could occupy interior cover. Within the spacing mechanism characteristic of coots, maximum possible nest densities occur on ponds under 2 ha when nests are located near shore.

Weller and Fredrickson (1973:287) showed that highest densities of coot nests on a 162-ha marsh in Iowa occurred when open water occupied about 50% of the area. Less open water resulted in fewer nests. Ponds on my area normally provided more than 50% open water in May when most nests were started. A few nest ponds became completely overgrown with

TABLE 3

AVAILABLE AREA FOR NESTING COOTS ON OCCUPIED PONDS

Available area per pair (ha)[a]	Percent of nesting pairs					
	>1 nest per pond			1 nest per pond		
	1973 (330)[b]	1974 (371)	1975 (773)	1973 (93)	1974 (184)	1975 (240)
to 0.10	0	0	2	5	8	15
0.11–0.20	23	8	16	26	17	27
0.21–0.30	46	24	43	12	13	13
0.31–0.40	8	14	21	16	15	22
0.41–0.50	12	16	13	10	11	6
0.51–0.60	6	12	3	9	7	4
0.61–0.70	3	10	t[c]	9	3	4
0.71–0.80	1	4	t	3	5	4
0.81–0.90	0	6	0	5	9	3
0.91–1.00	0	5	1	1	2	*t*
>1.00	1	1	t	4	10	2

[a] Pond area/number of nests.

[b] Number of nests.

[c] t = <0.5%.

whitetop later in the season and it is possible that this discouraged unsuccessful coots from renesting; data on this aspect are lacking.

Territory size was not measured, but data on maximum size were obtained. Considering ponds with 2 or more nesting pairs, over 60% of the pairs must have had territories under 0.3 ha in 1973 and 1975 (Table 3). This is supported by nest-to-nest distances. Circular territories with nests 50 m apart would have provided about 0.2 ha per pair—less when nests were near shore. The greater space available per pair in 1974 suggested that territories were larger then; however, distances between nests were not measured. Kornowski (1957) compared the sizes of 91 European Coot territories on 2 large wetlands—one rich in food resources and the other apparently not rich—and concluded that territory size was inversely related to food yield. On the other hand, Gullion (1953:180), who found that areas defended by 5 marked coot pairs on 2 California wetlands ranged from 0.22 to 0.56 ha and averaged 0.43 ha, believed that the main function of the territory was undisturbed reproduction.

On ponds with 1 nesting pair, the area available to a pair would not be influenced by other pairs. Thus, proportionately more solitary pairs were able to use areas under 0.2 ha than those pairs that shared ponds (Table 3).

Nesting cover.—Coots used emergent plants and other objects for nest support. In 1975, the main support materials for 1013 nests were: whitetop

(37%), willow (24%), cattail (21%), and sedge (9%). Earliest nests were started about mid-May and these usually were supported by dead cattails or flooded willows, the principal materials available then. When new growth of whitetop and sedge became available in late May and early June, these plants—particularly whitetop—were used more often. At this time they appeared to be preferred over flooded willows for nest support, perhaps because they allowed the coots to nest farther from shore.

Floating nests (7%) occurred in relatively deep water and were most often anchored to whitetop plants. Fewer than 1% of the nests were supported by the pond bottom. Such nests were in shallow water, usually near shore, so likely these would have comparatively low success due to predation and disturbance (Fjeldså 1973:122). There was 1 exceptional condition under which coots readily built bottom-supported nests in the absence of cover. On 26 June 1975, strong winds and rising water levels from heavy rain destroyed both coot nests and cover (mainly whitetop) on a few large ponds. Two days later, coots on these ponds were building structures near shore in shallow water; some eventually became nests. Apparently the territorial bond was so strong that, despite lack of cover, they remained to renest.

In nests supported by whitetop, cattail and sedge, 78% were constructed of the same material as comprised their support, a proportion similar to one given by Fredrickson (1970:448). Dead cattail was used in 29% of nests supported by whitetop and sedge. The latter were used in only 2% of cattail-supported nests. Cattail was the main material in 19% of the willow-supported nests, whitetop in 39%, and sedge in 40%.

Nearby nest material was not essential to nest-site selection; coots evidently carried components several meters to some nests, particularly those supported by willows. Vegetation was usually obtained from the pond but, on a few occasions, coots obtained it (including wheat straw) from dry land.

At 930 nests supported by plants, water depth averaged 70 cm (range = 8–152), and did not differ among plant species ($P > 0.05$, Duncan's new multiple-range test). However, depth at floating nests ($\bar{x} = 100$ cm, range = 34–142, N = 72, $P < 0.01$) was greater, and depth at bottom-supported nests ($\bar{x} = 19$ cm, range = 10–28, N = 6, $P < 0.01$) was less. These measurements were made in a year of high water levels, so are probably higher than would prevail in most years.

SUMMARY

American Coot nest densities on a 31.1-km^2 block during 1973, 1974, and 1975 were, respectively, 13.6, 17.8, and 32.6 nests/km^2. Consistent with territoriality in this species, nest numbers increased directly with pond size. Occupancy rate also increased with pond permanency, however, nest density on occupied ponds was independent of permanency type.

Only 2 of 1991 nests occurred on ponds that became dry before the young could have fledged. Close to one-half of the pairs occupied territories of less than 0.3 ha. There was some indication that territory size was influenced by available space, but this was not verified. In 1975, the distance to the nearest nest on the same pond ranged from 22 to 145 m ($\bar{x}$ = 54 ± 20 m, N = 577).

Most, if not all, coots attracted to the area apparently nested, though a small proportion of pairs delayed nesting until additional nest cover became available through new emergent plant growth. Territorial spacing and the distribution of nesting cover were the main factors governing nest distribution. Most ponds had sufficient cover to accommodate all the coot nests possible under the spacing behavior of this species.

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NESTING ECOLOGY OF ARCTIC LOONS

MARGARET R. PETERSEN

The Pacific Arctic Loon (*Gavia arctica pacifica*) nests in tundra and boreal forest regions of North America and northeast Siberia and is commonly found wintering along the Pacific coast of North America from the Gulf of Alaska to Baja California (Bent 1919, Dement'ev and Gladkov 1951, Palmer 1962). Information on the nesting ecology of Arctic Loons in North America is limited to a study at the McConnell River Delta, Northwest Territories (Davis 1972), a study at Storkersen Point, Alaska (Bergman and Derksen 1977), and incidental observations from other areas (Brandt 1943, Bailey 1948, Sutton and Parmalee 1956, Parmalee et al. 1967, Chiles 1969). Most information on nesting ecology is from European and Asian subspecies (*G. a. arctica* and *G. a. viridigularis*) (Gilroy 1923, Dement'ev and Gladkov 1951, Lindberg 1968, Sjölander 1968, Lehtonen 1970, Dunker and Elgmork 1973, Dunker 1974).

This study was designed to investigate the adaptations of the Arctic Loon in western Alaska to the tundra pool habitat. Specific objectives were to determine the habitat used by Arctic Loons during the breeding season, to observe reproductive success, and to evaluate factors influencing reproductive success.

STUDY AREA AND METHODS

A study area of 12.3 km^2 was established on the Clarence Rhode National Wildlife Range on the Yukon-Kuskokwim River Delta, Alaska (61°26'N, 165°26'W), about 24 km from the coast of the Bering Sea (see Mickelson 1975 for detailed description). The land vegetation types on the study area were wet marsh tundra and heath tundra as described by Holmes and Black (1973). The study area contained 266 lacustrine ponds varying from 0.2 ha to 100 ha, and averaging 1.5 ha in size. Most ponds were 0.5–1.5 m deep and contained small islands of the type used by nesting waterfowl and loons.

Loon nests were found by searching shorelines and wading to islands. All ponds were searched for nests prior to or during the time the eggs hatched, and twice thereafter for the presence of adults and young. Arctic Loon nests found without eggs or egg remains were considered to be nests which had contained eggs since Common Loons (*Gavia immer*) do not build a complete nest platform until the first egg is laid (Olson and Marshall 1952). Observations of the nesting behavior of Arctic Loons have verified that assumption (Petersen 1976). Laying dates of eggs for most nests were estimated by egg flotation (Westerkov 1950), or by interpolation from the dates of hatching. Sizes of ponds and distances between nests were measured from aerial photographs.

RESULTS

Spring phenology and loon arrival.—The ponds and river systems were covered with a complete layer of ice on my arrival on 3 May 1974, and on

TABLE 1
PHENOLOGY OF SPRING ICE MELT

Event	1974	1975
River with open leads	4 May	30 May
River ice-free	26 May	15 June
Sloughs draining meltwater	5 May	27 May
Ponds with meltwater	6 May	26 May
All ponds 90% or more ice-free	23 May	5 June

2 May 1975. Snow cover was also complete at this time in 1975, but most of the ground was bare in early May in 1974. Melting of ice and snow was later in 1975 than in 1974, but proceeded faster in 1975 than in 1974 (Table 1).

Arctic Loons were first observed on 5 May 1974, and 12 May 1975, with peak arrival dates of 23 May 1974, and 29 May 1975. Previous arrival data of Arctic Loons in an area within 9.6 km of the study area were: 12 May 1969 and 1970, and 23 May 1971 and 1972 (Mickelson 1973), and 17 May 1973 (C. P. Dau, pers. comm.). Pairs occupied the ponds (46 of 52 observations) as soon as sufficient meltwater or open water was available to enable the bird to take-off from them (6 May 1974, and 26 May 1975).

Nests and nest-sites.—Nineteen and 60 pairs of Arctic Loons nested on the study area in 1974 and 1975, respectively. Nests were oval in shape and made of materials from the vicinity of the nest. Nest-sites were categorized as one of 4 types: (1) islands which were surrounded by water during the entire nesting season; (2) drying islands which were surrounded by water at initiation of the clutch, but became connected to shore prior to hatching; (3) wet shore nests which were at the edge of emergent vegetation; or (4) dry shore nests. Although the total number of nests in the study area varied widely between the years, the use of shore and island nest-sites did not differ significantly ($\chi^2 = 1.53$, 1 df, NS). Most nests were

TABLE 2
ARCTIC LOON NEST-SITES

	Number of nests			
Year	Island	Drying island	Wet shore	Dry shore
1974	9	2	6	2
1975	21	4	30	5
Total	30 (38%)	6 (8%)	36 (46%)	7 (9%)

TABLE 3

DISTRIBUTION[1] AND DISTANCES BETWEEN ARCTIC LOON NESTS

Year	Number	Distance (m) Mean ± SE	Distance (m) Range	R	σ_{re}	C	P
1974	18	386 ± 41	134–590	1.218	0.034	2.029	0.0424
1975	58	297 ± 14	134–590	1.641	0.012	9.667	0.0001

[1] R is the measure of the degree the observed distribution deviates from random (R = 1 in random distribution, R = 0 in maximum aggregation, and R = 2.149 in uniform distribution); C is the standard variant of the normal curve; P is the level of significance (Clark and Evans 1954).

along wet shore, followed in frequency by nests on islands, dry shore and drying islands (Table 2).

Ponds with nests averaged 1.8 ± 0.4 ha (range 0.3–7.0 ha, N = 19) in size in 1974 and 1.8 ± 0.2 ha (range 0.3–9.6 ha, N = 60) in size in 1975. Only 2 ponds (<1%) on the study area were greater than 9.6 ha, and 24% were less than 0.3 ha.

Nests were evenly spaced in both years (Table 3), with straight line distances between nests averaging 23% greater in 1974 than 1975 (t = 2.60, 74 df, $P < 0.02$).

Clutch-size and chronology.—Clutch-sizes in 33 of the 79 nests could not be determined because predation had occurred before the nests were found. Forty-three nests contained 2 eggs and 3 contained 1 egg, for an average clutch-size of 1.93. The female from a nest containing 1 egg was collected 3 days after laying. She had 2 ruptured ovarian follicles, demonstrating that she had laid 2 eggs, 1 of which was not found. Possibly all of the loon nests had contained 2 eggs, and the other 1-egg clutches reflected the effects of partial predation.

Few dates of egg-laying could be estimated in 1974 because of almost complete destruction of clutches before the nests were found. Egg-laying occurred in 2 nests on 29 May and 2 June, respectively, 7 and 11 days after the peak arrival of pairs on ponds. In 1975 initiation of 36 clutches oc-

TABLE 4

DATES OF ARCTIC LOON EGG DESTRUCTION 1975

Status of eggs	Number of nests observed 4–18 June	Number of nests observed 19 June–3 July	Number of nests observed 4–20 July
Whole eggs	32	11	0
Eggs destroyed	10	23	8

TABLE 5
HATCHING SUCCESS OF ARCTIC LOONS BY NEST-SITE 1975

	Location of nests		
Nest fate	Island No. (%)	Drying island and wet shore No. (%)	Dry shore No. (%)
Successful	11 (52.4)	7 (20.6)	1 (20.0)
Destroyed	10 (47.6)	27 (79.4)	4 (80.0)

curred between 4–22 June with 50% of the nests begun by 9 June, 11 days after the peak arrival of pairs on ponds. Egg-laying was probably begun only about 7 days later in 1975 than in 1974.

Hatching success.—Only 1 of 19 nests (5%) hatched on the study area in 1974. In this nest 1 egg hatched on 25 June. At least 1 egg in 19 of 59 nests (32%) hatched in 1975. The first egg hatched on 1 July and the peak of hatching occurred on 4 July. All young hatched by 6 July, although the laying dates for 36 clutches indicated that 47% of the clutches should have hatched between 7 and 19 July. Two eggs hatched in 7 of the 19 (37%) successful nests, with the second egg hatching within 2 days of the first egg.

Exact dates of egg destruction could not be determined for most nests in 1974, but the contents of 3 of the 9 nests observed between 2 and 17 June, and 5 of 6 nests observed between 18 June and 4 July had been destroyed. This suggests that predation became heavier later in the incubation period and for nests initiated later as was obvious in 1975 ($\chi^2 = 28.08$, 2 df, $P < 0.005$; see Table 4).

Nests on islands were more successful than nests located in other sites in 1975 ($\chi^2 = 6.41$, 1 df, $P < 0.05$; see Table 5), although only 36% of the nests were on islands (Table 2). Island nest-sites were not established earlier than other types of nests ($\chi^2 = 0.91$, 3 df, NS).

Eggs were observed being destroyed only when human activity near the nest forced an adult off a nest for several hours and a Long-tailed Jaeger (*Stercorarius longicaudus*) and a Parasitic Jaeger (*Stercorarius parasiticus*) each ate 1 egg (D. G. Raveling, pers. comm.). Eggs from 3 nests were gathered by Eskimos for food. Glaucous Gulls (*Larus hyperboreus*) and Parasitic and Long-tailed jaegers nested in the study area and were frequently observed. Red foxes (*Vulpes fulva*) were commonly observed, and 1 arctic fox (*Alopex lagopus*) was seen. However, the species of predator that destroyed each loon egg was generally undetermined. Glaucous Gulls normally eat eggs at the nest, but occasionally may fly away from a nest with whole eggs before eating them. Jaegers normally eat eggs at a nest

TABLE 6
ARCTIC LOON NEST-SITE AND EVIDENCE OF PREDATION

Year	Appearance of destroyed nests	Number of nests			
		Island	Drying island	Wet shore	Dry shore
1974	Fragments	1	1	3	2
	Without fragments	3	1	1	0
	Unknown	5	0	0	1
1975	Fragments	5	3	5	0
	Without fragments	5	0	15	4
	Human destruction	0	0	3	0

(Mickelson 1975) and, if eggshells remain in a nest, loons may remove them and drop them into the water (Olson and Marshall 1951, Hall and Arnold 1966, and von Braun et al. 1968). Foxes remove eggs from the vicinity of a nest before eating or caching them (Tinbergen 1972), but fox tracks were rarely discernible in the vegetation.

Nonetheless, the evidence of the type of predation at different nest-sites (Table 6) varied significantly in 1975. Egg remains were found most often in, or near, island and drying island nest-sites, and nests without egg remains were predominantly shore nest-sites ($\chi^2 = 9.58$, 3 df, $P < 0.025$). This suggest that jaegers and gulls were primarily responsible for destruction of nests on islands, and foxes caused most of the destruction of those on shores. Data from 1974 are insufficient for testing differences by nest-site. However, the overall proportion of destroyed nests with egg remains to those without, was similar in both years ($\chi^2 = 2.02$, 1 df, NS).

DISCUSSION AND CONCLUSIONS

Factors influencing arrival and nest initiation.—Arctic Loons used the first available open ponds in spring. In the year in which ponds were available when loons arrived (1974) they were used immediately. In the late year (1975) loons were observed before ponds were available, but they only occupied ponds as soon as sufficient water was available. Thus, the timing of migration was not adjusted to compensate for the early or the late year, and may coincide with normal or average dates of availability of water areas. More data are needed for confirmation of this conclusion.

Lehtonen (1970) and Davis (1972) suggest that Arctic Loons wait for water levels to decline before laying eggs. Nest-sites were available by 18 May 1974, when Arctic Loons arrived, but loons did not begin laying until 29 May. Ponds in the spring of 1975 had dry shores by 1 June, but loons did not initiate nests until 4–22 June. Loons did not lay eggs when nest-sites were first available, suggesting that the delay in laying eggs is not necessarily a direct result of the availability of nest-sites.

Grau (1976) has shown that by counting the number of dark and light rings of the yolk after staining, the length of time for yolk formation can be estimated. An insufficient sample of loon eggs (N = 1) has been adequately examined, however, the similar-sized Cackling Goose (*Branta canadensis minima*) requires 12 days for yolk formation (Grau 1976). Yolk formation in the Arctic Loon may be initiated when the birds arrive on the nest pond, as the delay of egg-laying is about the same duration as the suspected time of development of the yolk. Such a delay is an adaptation to a widely fluctuating arctic environment, where ponds necessary for nesting may or may not be available when birds arrive. Shore and island nest-sites are not available until after water levels have declined in the ponds, usually several days after the pond has open water. The delay of egg formation insures that suitable nesting habitat will be available when the egg is ready to be laid and prevents the loss of eggs that might otherwise occur.

Factors influencing hatching success of Arctic Loons.—Hatching success appeared to be influenced most significantly by predation, which could be altered by nest-site selection, the timing of nesting, the type of predator, and the availability of alternate prey. In 1974, when 95% of nests were destroyed, hatching success was not related to the type of nest-site selected. In 1975, nest-site selection was an important factor in hatching success. The significantly higher success of pairs nesting on islands (Table 5) seems to represent selection pressure for loons to nest on islands. Although islands were available in 83% of the ponds used by nesting loons (N = 68), only 53% of the nests were located on islands. Of 43 ponds with shore nests, 38 (88%) contained 1 or more islands apparently suitable for nesting when loons began laying eggs, yet islands were not used.

The high rate of nest destruction by predators in 1974 may have resulted from a lack of alternate prey. Only 3 tundra voles (*Microtus oeconomus*) were seen during the entire 1974 field season, in contrast to daily observations of voles in 1975. Red foxes were frequently seen in both years, in contrast to 1 observation from 1969–1972 by Mickelson (1975) on an adjacent study area. Jaegers and Glaucous Gulls were almost always in evidence and apparently did not nest in 1974, but did in 1975.

The most abundant nesting waterfowl on the study area was the Cackling Goose. In 1974, Glaucous Gulls, jaegers, and red foxes destroyed 64% of 95 Cackling Goose nests (D. G. Raveling, unpubl. data), in contrast to a 33% average over 4 years recorded by Mickelson (1975). The 1974 modal hatching date of Cackling Goose eggs was 23 June with 93% hatching by 28 June. No Arctic Loon nest which would have had eggs hatch after 25

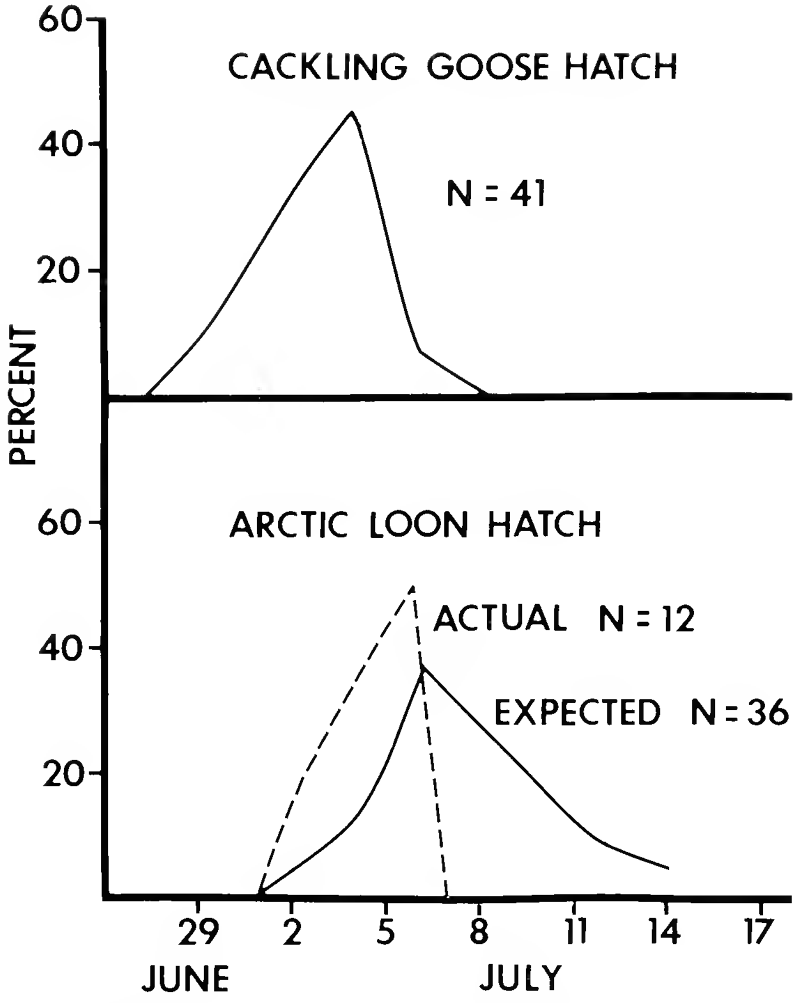

FIG. 1. Hatching dates of Cackling Goose and Arctic Loon eggs in 1975.

June was successful. In 1975, the modal hatching date of Cackling Goose eggs was 3 July, with all eggs hatching by 7 July. Arctic Loon eggs began hatching 1 July and should have continued hatching to 19 July, but none hatched after 6 July at which time the goose hatch was essentially complete (Fig. 1).

Jaegers and gulls commonly flew over ponds and apparently successfully found and destroyed cryptic loon eggs, especially in 1974, but this occurred primarily after the hatching of the creamy colored goose eggs which had been a common food source for jaegers. Combined island and shore nesting by loons may reflect an adaptive response by loons to varying predation pressures—by jaegers and gulls on islands and foxes along shorelines. In years of low or average fox density and average or high jaeger density, shore nesting may be favored. Conversely, when jaeger numbers or their taking of eggs is low, island nesting may be favored. In years of high combined avian and mammalian predation, density and pressure, and low vole density, such as 1974, Arctic Loons were almost totally unsuccessful.

Because of predation pressure, the timing of Arctic Loon and Cackling Goose hatching dates was an important factor in reproductive success of the Arctic Loon. Cackling Geese will normally be hatching before the majority of Arctic Loons because of their 11-day earlier nest initiation (Mickelson 1975, Raveling, unpubl. data), and shorter incubation period (26 vs 28 days) even though they lay eggs over a 4- to 6-day period, in contrast to the initiation of incubation with the laying of the first egg by loons. Arctic Loon eggs became the most abundant large eggs on the study area after the geese hatched. Heavy predation on loon eggs occurred late in incubation, when adults were less likely to leave the nest, than early in incubation. Davis (1972), at the McConnell River Delta, also noted an increase in predation on loon eggs when the eggs of nearby colonial Blue Geese (*Anser caerulescens caerulescens*) were hatching, but did not note if the increased predation pressure was significant.

SUMMARY

Arctic Loons were studied on the Yukon-Kuskokwim Delta, Alaska, from the time of their arrival in May to their departure in September, in 1974 and 1975. Pairs arrived on breeding ponds as soon as sufficient meltwater was available to allow their take-off and landing. Loons apparently do not initiate nests immediately after their arrival, even when nest-sites are available. Delayed egg-laying may be dependent on a period of yolk formation. Delaying yolk formation until after arrival on nest ponds is an adaptation by loons to the variable time suitable habitat becomes available for nesting.

Predation of eggs by Glaucous Gulls, Long-tailed and Parasitic jaegers and foxes varied in relation to the location of the nest-site, and the availability of alternate prey. Hatching success was the lowest recorded for Arctic Loons (5%) in 1974, when eggs of both loons and Cackling Geese were taken in large numbers by predators. Hatching success increased to 32% in 1975 when an abundance of tundra voles was observed. No loon eggs hatched after the hatching of the Cackling Goose eggs when this alternate prey was no longer available. Nests destroyed by foxes were predominantly along shorelines, and those by gulls and jaegers were predominantly on islands. Nest-site selection by Arctic Loons may reflect an adaptive response to varying selective pressures by their predators.

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Errata.—Vol. 91, No. 1, "Song differences and map distances in a population of Acadian Flycatchers" by R. B. Payne and P. Budde. An error in placing of decimals affects the numbers in Tables 1 and 2, p. 33. Values for characters 7 through 11 should be multiplied by 0.1 to correct the min, max, and means. The values for SD are also affected, but the values for CV and the results of the principal component analysis and the clustering analysis are not affected by the change.—R. B. Payne.

"Red-shouldered Hawk nesting ecology and behavior" by J. W. Portnoy and W. E. Dodge. On p. 104 the scientific name for Bald Eagle should read *Haliaeetus leucocephalus*.

Vol. 91, No. 2, "Effects of pine-oak clearcutting on wintering and breeding birds in southwestern Virginia" by R. N. Conner et al. On p. 307, Table 1, the scientific name of the Carolina Wren should read *Thryothorus ludovicianus*.

Vol. 91, No. 3, "Blue-winged × Cinnamon Teal hybrid from Oklahoma" by E. G. Bolen. On p. 367 the scientific name of the Cinnamon Teal should read *Anas cyanoptera*.

Vol. 91, No. 2, "Experiments on population regulation in two North American parids" by F. B. Sampson and S. J. Lewis. On p. 225, para. 3, line 7, the first BFL 2 should read BFL 1. On p. 227, the ANOVA used should read 1-way ANOVA.

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GENERAL NOTES

Evidence for vocal learning in prairie grouse.—Vocal learning may be defined as the ability of an individual to develop or modify songs or calls through reception of external stimuli. The phenomenon has been studied primarily in passerines and parrots but may occur in other groups. Nottebohm (Am. Nat. 106:116–140, 1972), however, suggested that learning was restricted to only a few taxa and specifically mentioned galliforms as a group in which it was not expected. Reasons for this supposed absence included proximity to early avian ancestors (with the assumption that vocal learning is recently evolved), apparent genetic rigidity in domestic chicken (*Gallus* sp.) vocalizations (Schjelderup-Elbe, Z. Psychol. 92:60–87, 1923; Konishi, Z. Tierpsychol. 20:349–367, 1963), and simple syringeal structure.

In this paper I describe circumstantial evidence for vocal learning in Greater Prairie Chickens (*Tympanuchus cupido*) and Sharp-tailed Grouse (*Pedioecetes phasianellus*) and discuss its potential significance. The evidence comes from a study of behavior and isolating mechanisms between the species in northwestern Minnesota (Sparling, unpubl.).

Observations were made from blinds located on peripheries of 4 display grounds during the breeding seasons of 1975–1978. Additional observations were made on 1 F1 hybrid, 5 prairie chicken and 8 sharptail males raised in captivity from hatching. Display grounds were named for local landmarks and included the Pankratz (1 F1 hybrid, 14 prairie chicken males), Pembina (1 F1 hybrid, 1 sharptail and 22 prairie chickens), WTymp (1 F1 hybrid, 1 sharptail and 5 prairie chickens) and TJct (5 sharptails with an F1 hybrid visiting for 2 weeks in 1975). Of the birds discussed in this paper, all captives, all wild sharptails and 8 wild prairie chickens were individually banded. Although none of the F1 hybrids were banded, they could be readily recognized by plumage and behavioral peculiarities.

Vocalizations were recorded at 19 cm/sec with a Uher 4000 Report-L tape recorder and Uher omnidirectional and Sennheiser ultra-unidirectional microphones. A Kay Elemetrics Co. 7029-A sound spectrograph set at 20-2000 and 40-4000 Hz ranges, with wide and narrow band settings, was used for sound spectrograms. Playbacks were made with a Uher 4000 Report-L tape recorder and Nagra DH speaker-amplifiers set within the centers of territories.

Evidence for vocal learning came from 3 independent sources. First, all male prairie chickens were heard to imitate a 3-note call that was characteristic of hybrids. The call was initially heard in 1975 from male hybrids on the Pankratz and TJct display grounds and subsequently from all F1 hyhrids throughout the study. However, it was not heard from prairie chickens until late May 1976 when 1 bird on the Pankratz display ground gave it. By late spring 1977 all male prairie chickens on the Pembina and most of those on the Pankratz and WTymp display grounds used it in agonistic encounters. All captive male prairie chickens housed with a subdominant hybrid male since hatching also gave the vocalization, but prairie chickens on grounds without hybrids were never heard to give it. Prairie chicken 3-note calls were similar to "whines" (Fig. 1, Table 1); the major differences between these calls and those of hybrids included number of notes per bout, mean note duration, strongest frequency and a pronounced chevron form of frequency modulation in 3-note calls. Presumably, prairie chickens either learned the 3-note call or modified their "whines" to match the hybrids'.

The second example of learning was found in the "coos" of the Sharp-tailed Grouse. "Coos" are often used in advertisement and function as tonic signals. They are characterized by note durations of 0.22 ± 0.08 sec and internote intervals of 3.40 ± 4.09 sec (N = 11 individuals and 306 sequences). In some playback experiments I altered the normal temporal pattern of "coos" so that 2 notes were joined and a third preceded these by 0.09 sec (Fig. 2). Note durations were 0.17 and 0.35 sec, respectively. Thus, hoth internote interval and

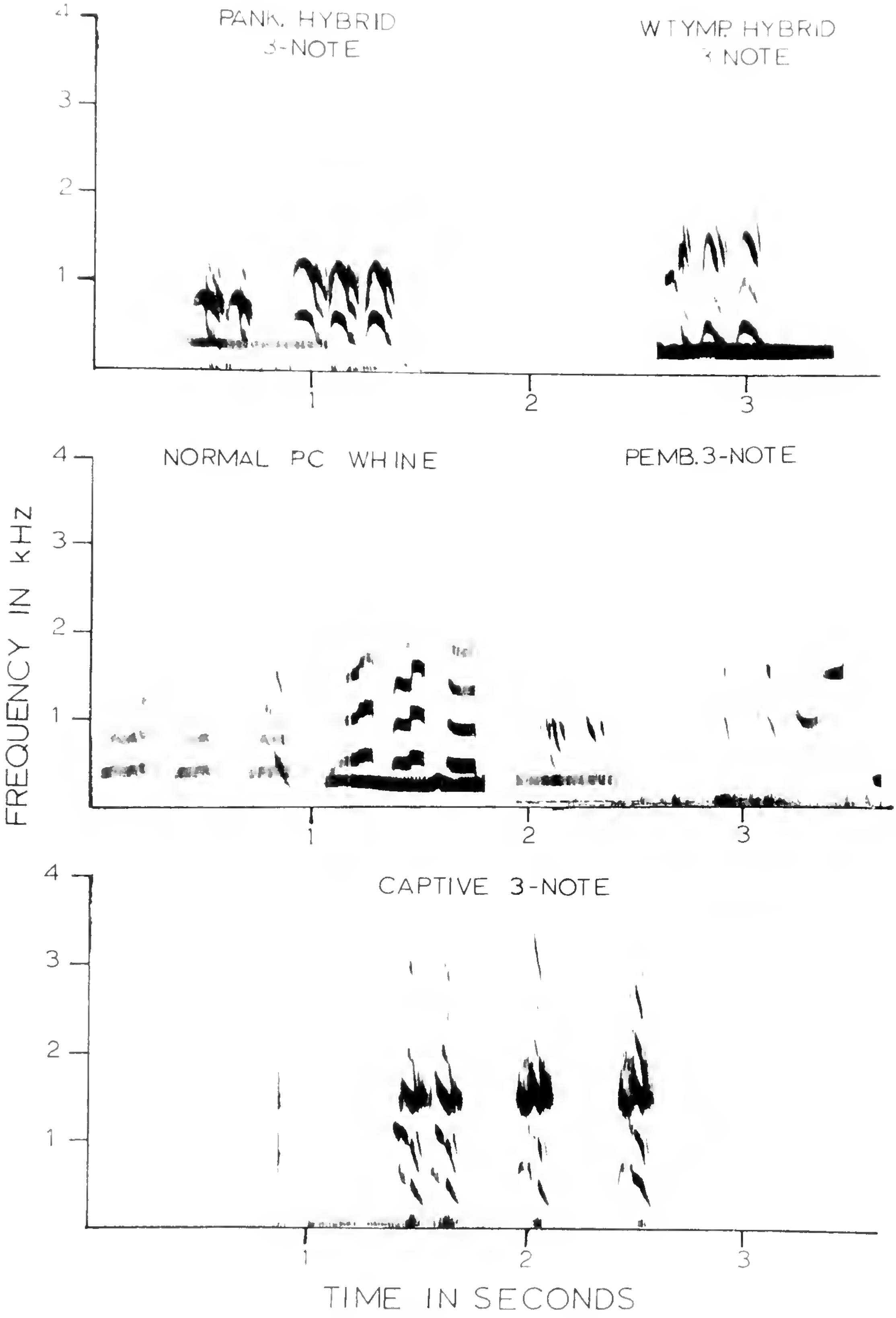

FIG. 1. Sound spectrograms of F1 (Pankratz and WTymp hybrid) and prairie chicken (Pembina and captive) 3-note calls and prairie chicken (Normal PC "whine") "whines." Dark lines near 300 Hz in Pankratz hybrid, WTymp hybrid and Normal PC "whines" are "booms" from other birds.

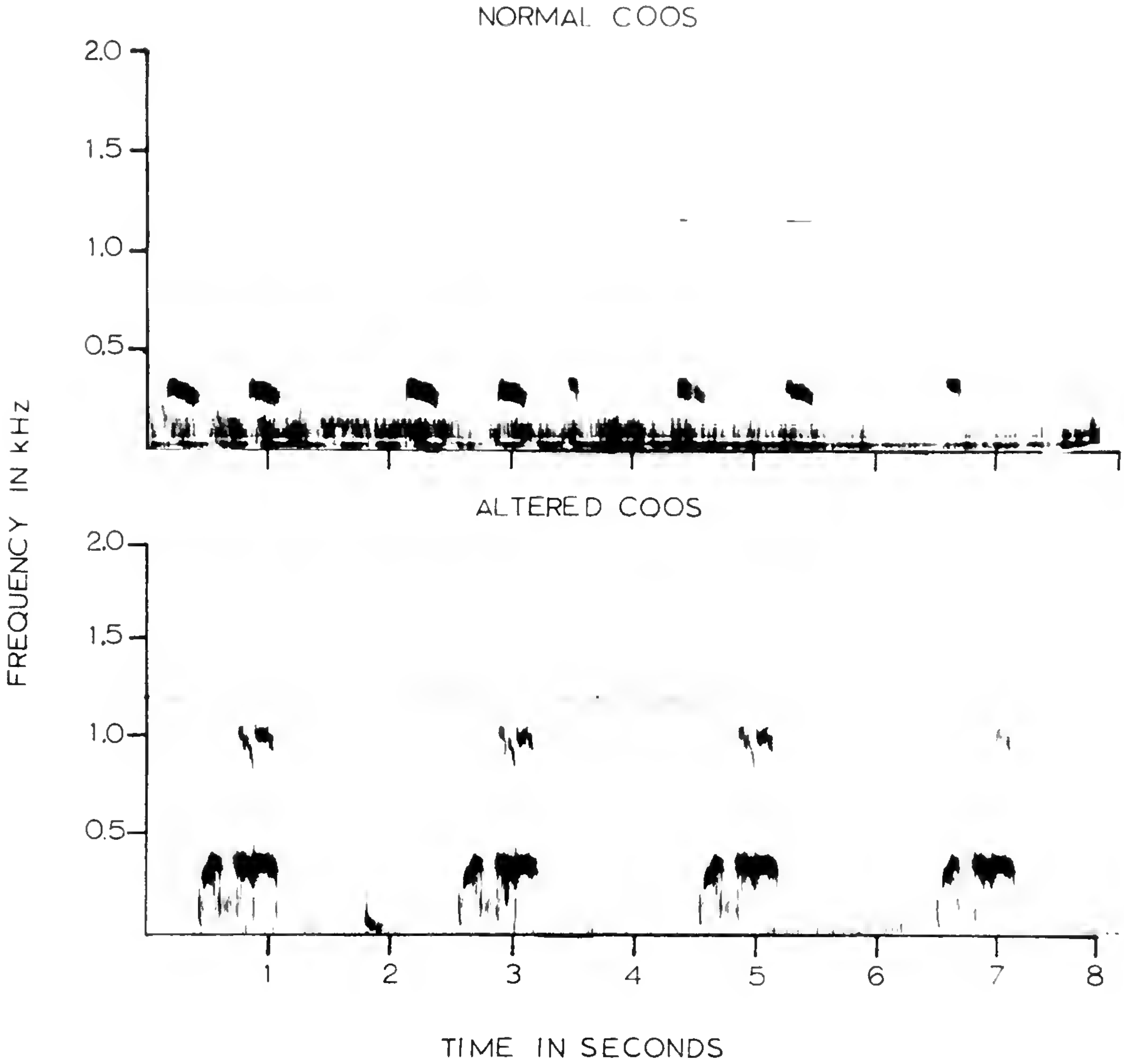

FIG. 2. Sound spectrograms of typical sharptail cooing and the altered playback of cooing. Light marks at top of sonagrams are amplitude displays.

note duration were outside the typical range for "coos." This altered sequence was played 8 times over a period of 5 days on the TJct display ground. During the sixth playback the male being tested mimicked the call so faithfully that his calls could not be distinguished from recorded ones.

The third example of learning was from hybrids. The Pankratz hybrid was on an all-prairie chicken display ground and, although he occasionally gobbled (a sharptail vocalization), most of his behaviors closely resembled those of prairie chickens. The WTymp hybrid, however, gave prairie chicken displays when confronting prairie chickens but switched to sharptail displays when fighting with the sharptail. Typical prairie chicken-like calls in this bird's repertoire were "whoops" and "cooms" (an abbreviated form of "boom"); sharptail vocalizations included "coos," "chilks" and "gobbles." The parentage of these hybrids was unknown but both appeared to be F1's based on their intermediate plumage.

Although the evidence presented here is not unequivocal, it indicates that prairie grouse may be able to learn some vocalizations and modify others through experience. Further

TABLE 1
CHARACTERISTICS OF 3-NOTE CALLS AND "WHINES" FROM HYBRIDS AND PRAIRIE CHICKENS

Characteristic		Pankratz hybrid 3-note (N = 9)[c]	WTymp hybrid 3-note (N = 20)	Prairie chicken 3-note (N = 34)	Prairie chicken "whines" (N = 42)
Number of notes	$\bar{x}$	3.24	3.33	2.83	9.24
	SD	0.01	1.03	0.39	9.10
Note duration[a]	$\bar{x}$	0.15	0.27	0.28	0.19
	SD	0.01	0.05	0.06	0.06
Internote interval[a]	$\bar{x}$	0.03	0.12	0.11	0.20
	SD	0.02	0.13	0.07	0.09
Strongest frequency[b]	$\bar{x}$	501	904	1547	989
	SD	52	190	17	542
Frequency modulation[b]	$\bar{x}$	338	258	122	281
	SD	43	199	63	155

[a] Temporal measurements in sec.
[b] Frequency measurements in Hz.
[c] Reported N are for number of sequences analyzed; 12 and 9 prairie chickens were used for 3-note calls and "whines," respectively.

research is needed before the importance of learning in these species is understood, but some speculation is possible. Vocal learning in these species suggests that their communicatory behavior is more plastic than predicted. Further, learning could promote dialect formation among display grounds which would facilitate recognition of strangers. This recognition may reduce overt aggression among regularly attending males. Interspecific territoriality could also be enhanced by imitation of heterospecific aggressive signals as suggested by the imitation of 3-note calls by prairie chickens and by behavioral switching in the hybrid.

The National Geographic Society, Sigma Xi, Norman Pankratz Conservation Fund and North Dakota Wildlife Federation, Grand Forks Chapter, provided funds supporting this research. Additional support was given by the Department of Biology, University of North Dakota and by the Agricultural Division of the Technical College and Northwest Experiment Station, University of Minnesota, Crookston. L. Oring, D. Svedarsky, C. Keller, C. Braun and D. Jones read the manuscript and offered valuable criticism. I especially thank C. Steinhauer for his assistance in raising the captive grouse.—DONALD W. SPARLING, *Cooperative Wildlife Research Laboratory and Dept. Zoology, Southern Illinois Univ., Carbondale, Illinois 62901.* (Present address: *Dept. Biology, Ball State Univ., Muncie, Indiana 47306.*) *Accepted 5 Jan. 1979.*

Wilson Bull., 91(4), 1979, pp. 621–623

Common Redpolls using spruce seeds in northern Utah.—During winter in the United States and southern Canada, the Common Redpoll (*Carduelis flammea*) generally is considered a bird of open woodlands, weed patches, fields, and brushy fence rows, where it feeds mainly on birch (*Betula*) and alder (*Alnus*) seeds (Godfrey, The Birds of Canada, Nat. Mus. Bull. No. 203, 1966). Thus, in a mixed flock with 30 White-winged Crossbills (*Loxia leucoptera*) and several Pine Siskins (*Carduelis pinus*) on 30 November 1977, 26 km east of Preston, Franklin Co., Idaho, I was surprised to see 25 Common Redpolls feeding on cones at the top of Engelmann spruce (*Picea engelmannii*). At 13:00 on 7 December 1977, I found 25 Common Redpolls and 25 Pine Siskins feeding on spruce cones in the Bear River Mountains (elev. = 2500 m), Cache Co., 18 km west of Laketown, Utah. I collected 2 males and 1 female from this flock. Previously, only 3 specimens of redpolls had been collected in Utah, but sight records have increased in recent years (Hayward et al., Birds of Utah, Great Basin Nat. Mem. 1, 1976). Several other mixed flocks containing 20–50 redpolls were seen that day.

Upon preparing the specimens (deposited in the collection at Utah State University), I found only hulled Engelmann spruce seeds in the esophageal diverticula (Fisher and Dater, Auk 78:528–531, 1961). Spruce seeds have rarely been mentioned as food of the Common Redpoll in North America (Martin, Ecology 41:126–140, 1960; White and West, Oecologia 27:227–238, 1977), which is certainly enigmatic since spruce seeds are commonly reported as food of Common Redpolls in Europe (e.g., Svärdson, Br. Birds 50:314–343, 1957; Eriksson, Ann. Zool. Fenn. 7:273–282, 1970; references in Newton, Ibis 109:33–98, 1967).

The 3 diverticula contained 120, 52, and 41 seeds. Such variation is not unusual (White and West, op. cit.) since the diverticulum may be filled and emptied several times a day in winter (Brooks, Auk 95:182–183, 1978). (Note that this does not represent triphasic feeding as described in Brooks [op. cit.] since all the seeds were hulled.) The total seed contents of each diverticulum weighed 0.27, 0.14, and 0.12 g, respectively, when dried to constant weight at 60°C. A caloric value of 25.98 ± 0.17 kJ/g (N = 4, ± 1 SD) was obtained from the Engelmann spruce seeds using a Phillipson microbomb calorimeter. Therefore, the 3 redpolls had 7.02, 3.64, and 3.12 kJ of energy stored, which represents 7.3, 3.8, and 3.2% of the daily energy budget (based on a daily energy need of 96.23 kJ [cited in White and West, op. cit.]). The amount of energy stored in the diverticulum represents only a small proportion of the Common Redpoll's daily energy needs (White and West, op. cit.).

Brooks (Wilson Bull. 80:253–280, 1968) stated that since Common Redpolls specialize on birch and alder seeds which "are substantially higher in caloric value than most types [of seeds] which have been measured. . . the adaptive value of the redpoll's selectivity of birch seeds in the wild is self-evident." Birch seeds contain only 23.01 kJ/g of energy (White and West, op. cit.), whereas hulled seeds of most conifers have caloric contents in excess of 25.10 kJ/g (see Table 7, Vander Wall and Balda, Ecol. Monogr. 47:89–111, 1977). Spruce seeds also contain twice as much protein and oil as birch seeds (Jones and Earle, Econ. Bot. 20:127–155, 1966), although the nutrient content of spruce seeds can vary considerably geographically (Pulliainen, Ann. Zool. Fenn. 8:326–329, 1971). Hence, use of high energy conifer seeds would increase the efficiency of the diverticulum, since a finite number of seeds can be stored at any given time. Using a diverticulum capacity of 2 g of seed, 20% water content in the seeds, and a redpoll assimilation efficiency of 70% (see White and West, op. cit.), plus the caloric content of 25.98 kJ/g for spruce seeds, the redpoll would gain over 4 kJ/g of seed consumed by using spruce seeds rather than birch seeds. This gain could be even greater since conifer seeds contain only small amounts (<5%) of moisture (Botkin and Shires, New Mex. Exp. Sta. Bull. 344:3–14, 1948). However, if conifer seeds are not as easily digested as birch seeds, then assimilation efficiency might be lower.

White and West (op. cit.) and C. White (pers. comm.) argue that redpolls use birch and alder because seed are: (1) abundant and predictable; (2) available all winter; (3) the correct size for the redpoll's small bill (see Newton, Finches, pp. 103–106, Taplinger Pub. Co., N.Y., N.Y., 1973); and (4) of adequate caloric content. Also, redpolls avoid competition with other finches and red squirrels (*Tamiasciurus hudsonicus*) (Brink and Dean, J. Wildl. Manage. 30:503–512, 1966) for conifer seeds by taking birch and alder seeds. Since redpolls show no hypothermic tendencies (Chaplin, J. Comp. Physiol. 89:321–330, 1974), in order to maintain a normal body temperature (>40°C) at very low ambient temperatures (West, Comp. Biochem. Physiol. 43A:293–310, 1972) they may have to consume as much as 42% of their body weight in 1 day (White and West, op. cit.). A very reliable food source is therefore important and redpolls are probably very sensitive to changes in food abundances.

Bock and Lepthien (Am. Nat. 110:559–571, 1976) found that the Common Redpoll is one of the most synchronously irrupting boreal seed-eating birds in North America, suggesting that widespread seed failure causes many redpolls to move southward (see also Kennard, Bird-Banding 47:231–237, 1976). Redpolls leave the Fairbanks, Alaska, area when birch and alder seed crops fail rather than switching to spruce (C. White, pers. comm.), suggesting that redpolls do not use spruce seeds on their usual wintering grounds. I suspect that spruce seeds are an important secondary food source for Common Redpolls when they are forced out of northern latitudes (see also Clement, U.S. Nat. Mus. Bull. 237:407–421, 1968). At the time of my study the spruce crop in northern Utah was at its highest peak in 30 years, with some trees bearing over 4000 cones (see Smith, West. Birds 9:79–81, 1978). Redpolls may only use the high-energy spruce seeds whenever they are abundant and easily gathered. Also, redpolls may switch to spruce when other preferred seeds are unavailable. Neither birch nor alder are present near my study area, nor were weed seeds available when the redpolls were collected, due to several feet of snow. Another possibility is that northern cones are inferior in quality compared to southern cones as shown by Pulliainen (op. cit.) in Finland, which would affect the efficiency with which cones could be used in the north.

The birds I observed did not appear to have any trouble manipulating spruce cones, so that an energy loss due to differential foraging time (Norberg, J. Anim. Ecol. 46:511–529, 1977) on spruce as opposed to birch would be minimal, provided that spruce cones are abundant. As with Pine Siskins, redpolls, while hanging upside down—either on the cone itself or from the branch to which the cone was attached, extracted seeds from the open cones. Since crossbills were extremely common during 1977 (Smith, op. cit.), the siskins and redpolls may have possibly relied to some extent on cones already opened by crossbills (see Turček, Ibis 98:24–33, 1956).

Keith Dixon was helpful during all stages of this study, and Clayton White made many helpful suggestions on an early draft, as did William Behle and Stephen Vander Wall. George West, Alan Knox, and Declan Troy made many helpful comments as referees. Bette Peitersen did the calorimetry work. This research was supported by NSF Grant DEB-75-13966 to James A. MacMahon.—KIMBERLY G. SMITH, *Dept. Biology and Ecology Center, UMC 53, Utah State Univ., Logan, Utah 84322.* *Accepted 2 Jan. 1979.*

Wilson Bull., 91(4), 1979, pp. 623–625

Small mammals and birds as food items of Ring-billed Gulls on the lower Great Lakes.—Vermeer (Can. Wildl. Serv. Rep. Ser. 12:1–52, 1970) noted the importance of rodents, mostly the meadow vole (*Microtus pennsylvanicus*), in the diet of Ring-billed Gulls (*Larus delawarensis*) in Alberta, Canada. In contrast, for Ring-billed Gull colonies on Lakes Michigan and Huron, Ludwig (Great Lakes Res. Div., Univ. Mich., Publ. No. 15:80–89, 1966) did not mention the presence of small mammals in his food collections. Jarvis and Southern (Wilson Bull. 88:621–631, 1976) noticed only 1 vole (*Microtus* sp.) regurgitated by an adult Ring-billed Gull during 12 years of observation (1963–1974) at the Roger City, Lake

Huron colony. However, in 1975 they noted *Microtus* sp. remains in 2 food samples (W. E. Southern, pers. comm.). Haymes and Blokpoel (1978) found that regurgitations of Ring-billed Gull chicks at the Toronto Outer Harbour rarely contained mammal remains—in 2 cases meadow voles and in 1 case deer mouse (*Peromyscus maniculatus bairdii*) (Can. Field-Nat. 92:392–395, 1978).

While censusing Ring-billed Gull colonies on the lower Great Lakes system we noted pellets in and around the nests. Those pellets contained remains of insects, fish, birds and mammals. Pellets containing mammal remains were generally of 3 types: tightly packed ovals of fur and bones, whole and flattened specimens and small balls of fur. Pellets containing bird remains were usually ovals of packed bones and feathers. Many of the pellets with bird and mammal remains were still moist, suggesting that they were freshly cast.

We collected pellets with mammal and bird remains during May and June 1977 in 4 colonies: the Canada Furnace yards at Port Colborne, Ontario, at the eastern end of Lake Erie; Grassy Island on the Niagara River; Leslie St. Spit (the eastern headland of Toronto Outer Harbour) on western Lake Ontario; and Strachan Island near Cornwall, Ontario, on the upper St. Lawrence River.

To quantify the occurrence of pellets containing mammal and bird remains, we arbitrarily selected a point in the colony and collected all such pellets in and around the first 100 nests that we encountered while moving away from the original point. At Port Colborne we sampled 400 nests over 3 collection dates and at Leslie St. Spit we sampled 900 nests over 5 collection dates. Each 100-nest sample was taken from a different part of the colony. At the Grassy Island colony we collected pellets from only 80 nests. At the Strachan Island colony we did not quantify the occurrence of pellets.

We collected a total of 107 pellets containing mammal remains near 400 nests ($\bar{x}$ = 0.268 pellets per nest) at the Canada Furnace colony, 18 pellets near 80 nests ($\bar{x}$ = 0.225) at Grassy Island and 14 pellets near 900 nests ($\bar{x}$ = 0.016) at Leslie St. Spit. At Strachan Island we collected 15 pellets.

The observed inter-colony differences in the occurrence of pellets with mammal remains may reflect the relative availability of small mammals and other food sources at the colonies concerned. For instance, the infrequent occurrence of pellets containing small mammal remains at Leslie St. Spit on the Toronto waterfront may reflect the low availability of small mammals in a large metropolitan center. Conversely, it may indicate an abundance of, or preference for, other food sources.

Mammal remains in the 83 pellets that contained skulls or jaws were identified by skeletal and dental characteristics. The meadow vole was the most common species, comprising more than 80% of those identified. The remainder were short-tailed shrew (*Blarina brevicauda*) and *Peromyscus* spp.

In addition to the 154 pellets of mammal remains, we collected 8 pellets with remains of birds. Remains in 5 pellets could be identified to species: Spotted Sandpiper (*Actitis macularia*, a chick), Savannah Sparrow (*Passerculus sandwichensis*), White-throated Sparrow (*Zonotrichia albicollis*) and Song Sparrow (*Melospiza melodia*, in 2 pellets). One pellet contained remains of *Oporornis* sp. (probably Mourning Warbler [*O. philadelphia*]) and another consisted of remains of *Melospiza* sp. (probably Swamp Sparrow [*M. georgiana*]). The eighth pellet contained remains of a Chipping Sparrow (*Spizella passerina*) and of a small unidentified emberizid. W. E. Southern (pers. comm.) observed songbirds being pursued and captured by Ring-billed Gulls and noted the presence of mummified songbird carcasses in Ring-billed Gull colonies on Lake Huron.

T. Hince and R. J. Prins assisted in the field. D. B. Campbell helped to identify the mammal remains. H. Ouellet identified the bird remains. J. E. Bryant and S. G. Curtis

commented on an earlier draft.—HANS BLOKPOEL, *Canadian Wildlife Service, Ontario Region, 1725 Woodward Drive, Ottawa, Ontario, Canada K1G 3Z7*, AND GERARD T. HAYMES, *Ontario Hydro, Aquatic Biology Section, 800 Kipling Avenue, Toronto, Ontario, Canada M8Z 5S4.* *Accepted 15 Feb. 1979.*

Wilson Bull., 91(4), 1979, pp. 625–626

Premigratory fat in the American Kestrel.—Premigratory fat deposition has been reported in many avian families (King and Farner, Annu. N.Y. Acad. Sci. 131:422–440, 1965), but I do not know of any previous report of it among the Falconiformes.

Methods.—Fourteen adult males, 1 immature male, 7 adult females and 1 immature female American Kestrel (*Falco sparverius*) were trapped in Balchatri traps in Cache County, Utah, in April, July, and September of 1973 and 1974. Birds were transported to the laboratory at Utah State University, and weighed to the nearest 0.1 g. Each was then sacrificed in an atmosphere of N_2, frozen and stored. Later, each carcass was vacuum dried at 5 mm Hg for a minimum of 3 days to constant weight. To facilitate drying, the body cavity was opened and the pectoral muscles were macerated. Each carcass was chopped into small pieces and the fat extracted in a Soxhlet apparatus using petroleum ether (B.P. 60–80°C) as the solvent, and dried to constant weight in a hot-air oven at 80°C. The weight of body fat was equated with the vacuum-dried weight minus the dry weight of the fat-extracted carcass (i.e., the fat-free dry weight). Student's *t*-test was used to compare any 2 means.

Results.—Body fat of males decreased from April to early September, then increased sharply in the latter half of September (Fig. 1). Body fat of females decreased from April to late July and increased steadily during September.

The average weight of body fat on males expressed as a percentage of body weight was about 4% in April. In July it was 3–4% for both males and females. Females had significantly more fat than males in September (7.0 and 5.3%, respectively).

The pattern of seasonal change in fat levels in the kestrel is typical of a migrant, i.e., the lowest level occurs soon after the breeding season in mid-summer and rapid deposition of fat occurs preceding and/or during the southward migration in the fall. The timing of the southward migration was identified by the disappearance of color-marked summer resident birds from the county. In spring, kestrels that winter south of Utah begin to arrive in Cache County between the last week of March and the first week of April. The summer population of adult kestrels in Cache County is about 10 times larger than the winter population. The population decreases noticeably in mid- to late September as the summer resident kestrels move southward. Banding records show that some individuals that summer in northern Utah migrate to Mexico (Gessaman, unpubl. data). The birds collected in September may represent a mix of summer residents in northern Utah and others which had bred at locations further north.

The percentage of fat in kestrels immediately preceding or during the fall migration is significantly less than the 15–50% reported for land birds that migrate over large bodies of water or extensive desert areas (Odum, Science 123:892–894, 1956; Ward, Ibis 105:109, 1963). The kestrel's fall migratory routes likewise do not pass over these kinds of barriers (Bent, Life Histories of North American Birds of Prey, Pt. 2, U.S. Natl. Mus. Bull. 170, 1938).

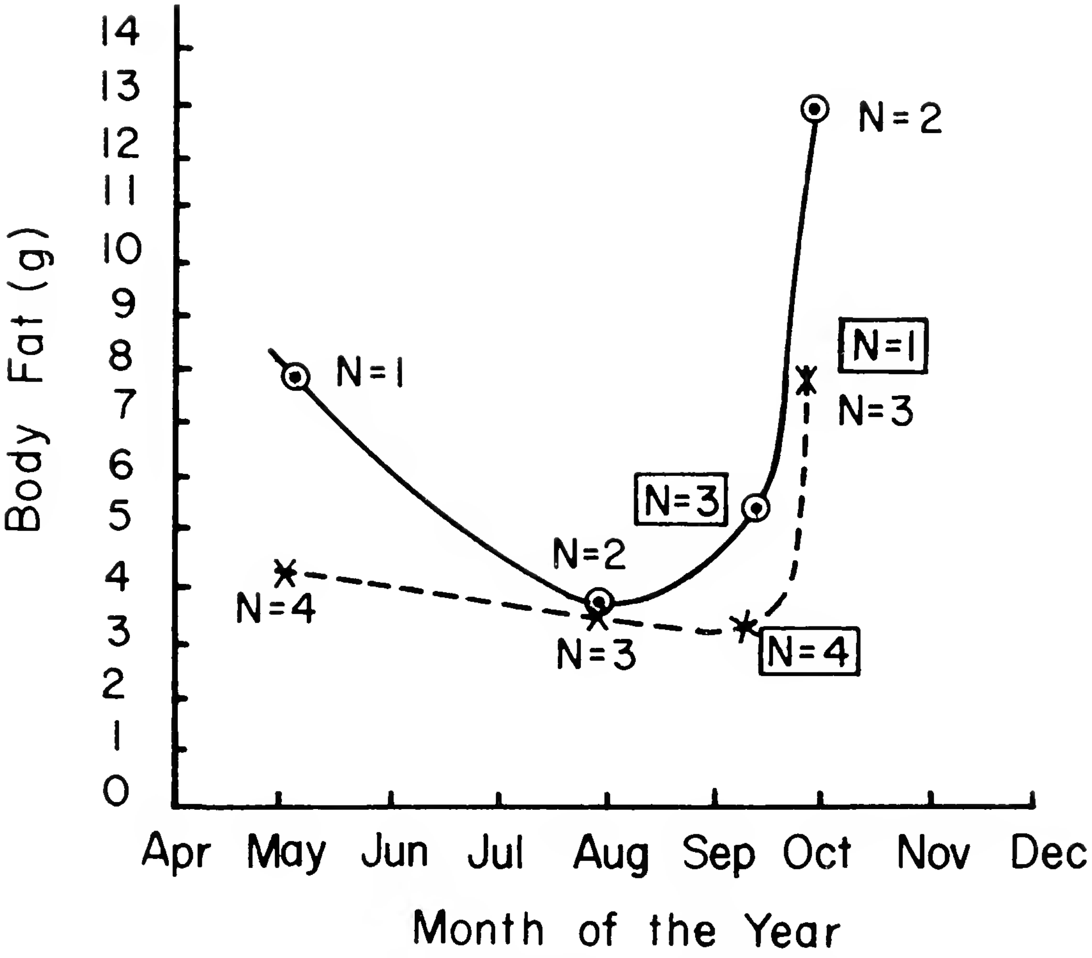

FIG. 1. Seasonal changes in body fat of kestrels in northeastern Utah. Boxed Ns represent birds trapped in 1973; Ns are birds taken in 1974, solid lines are males and dashed lines females.

This work was supported by NSF Grant GB 40109. Scott W. Sawby contributed significantly to this project. I wish to thank David W. Johnston for suggesting improvements in the original manuscript.—JAMES A. GESSAMAN, *Dept. Biology and Ecology Center, UMC 53, Utah State Univ., Logan, Utah 84322.* *Accepted 8 Dec. 1978.*

Wilson Bull., 91(4), 1979, pp. 626–628

First reports of pellet ejection in 11 species.—Pellet casting, widespread in birds of prey, also occurs in other groups. Birds whose foods contain indigestible hair, bone, shell, chitin, etc. are most likely to eject pellets. Hanson (List of species known to eject pellets, the International Bird Pellet Study Group, Bull. 7, with additions, 1977) reported pellet casting in 18 orders comprising 67 families and 316 species. One hundred and twenty-nine (41%) species were Falconiformes and Strigiformes. Stenzel (Using pellets to study bird diets, Point Reyes Bird Observatory News Letter, No. 36, 1975) mentions the Long-billed Curlew (*Numenius americanus*) and the Black Turnstone (*Arenaria melanocephala*) which were not listed by Hanson.

TABLE 1

SPECIES OF BIRDS OBSERVED CASTING PELLETS AND MEASUREMENTS OF SOME COLLECTED PELLETS FOR 6 SPECIES

Species	Location	No. collected	Length (mm) range	Length (mm) $\bar{x}$	Diameter (mm) range	Diameter (mm) $\bar{x}$
White Ibis (*Eudocimus albus*)	in flight					
Black-bellied Plover (*Pluvialis squatarola*)	beach					
Willet (*Catoptrophorus semipalmatus*)	beach	7	24–35	30	13–20	16
Greater Yellowlegs (*Totanus melanoleucus*)	mud flat					
Sanderling (*Calidris alba*)	beach	5	9–14	11	6–8	7
Laughing Gull (*Larus atricilla*)	beach					
Least Tern (*Sterna albifons*)	captive beach	4	13–16	14	9–11	10
Sandwich Tern (*Sterna sandvicensis*)	beach	4	18–25	21	11–15	14
Royal Tern[1] (*Sterna maximus*)	beach	11	17–35	27	12–25	19
Sooty Tern[2] (*Sterna fuscata*)	captive beach					
Black Skimmer (*Rynchops niger*)	beach	4	27–32	30	17–21	19

[1] Royal Tern pellets—body of pellet measured.

[2] Sooty Tern pellets collected on Dry Tortugas.

Between 1975 and 1978 I found pellet ejection in 11 species not listed by Hanson (op. cit.) including a skimmer (*Rynchops*) thus adding the Rynchopidae to the total number of families. Species were added to my list by direct observation (sometimes with collection of pellets in the wild) and by collection of pellets from captive individuals. The 11 previously unlisted species are shown in Table 1. My observations are mostly from the vicinity of Naples, Florida.

Pellets seem most numerous in roosting places, i.e., tops of wooden pilings and connecting stringers, beaches and sand bars.

I have found pellet ejection difficult to observe. Hours of observation are required to see a few instances of ejecting behavior. The behavior most often resembles the retching that accompanies regurgitation. Most pellet ejection by Willets that I have watched has taken 12–25 min. The Willet stands in a hunched position with fluid dripping from the bill, often flicking its bill sideways. As ejection becomes imminent the dripping and flicking increases.

then with 1 or 2 retches the bird deposits a pellet between its feet. At other times I have seen Black-bellied Plovers, Willets and Sanderlings flick their heads sideways and eject a pellet without any other casting behavior. One White Ibis ejected in flight, flicking its head sideways to cast the pellet. I have seen retching behavior in Snowy Egrets (*Egretta thula*) and Ring-billed Gulls (*Larus delawarensis*) suggesting that these 2 species may also eject pellets.

The pellets were generally ovoid but varied in size and shape in different species. Shorebird pellets were elongated, tern pellets almost round, and gull pellets teardrop-shaped. Pellets of different species may also vary considerably in size (Table 1). Royal Tern pellets were large and consisted of an ovoid body often with a long fin projecting like a tail. Measurements of the pellets of this species are for the body only, as inclusion of the tail would overestimate the real pellet size.

Pellets I examined were composed mostly of indigestible material. Tern and skimmer pellets resembled each other closely, containing mainly fish scales, bones, and fins. One Royal Tern pellet contained pieces of crab carapace and legs. Shorebird pellet composition varied considerably. Some shorebird pellets were composed completely of whole and crushed shell of coquina (*Donax variabilis*). I have seen this type of pellet ejected by Black-bellied Plovers, Willets, and Ruddy Turnstones (*Arenaria interpres*) and it is impossible to differentiate among the pellets of these species. At other times these 3 species eject pellets that seem to be composed mostly of chitinous material. Gull pellets not only contain indigestible parts of food items, but occasionally bits of glass, plastic and metal.

I wish to thank Oliver L. Austin, Jr. for his encouragement and constructive criticism during the preparation of this manuscript.—THEODORE H. BELOW, *3697 North Road, Naples, Florida 33942. Accepted 31 Jan. 1979.*

Wilson Bull., 91(4), 1979, p. 628

Rufous-collared Sparrow victimized by Bronzed Cowbird.—On 4 July 1977, on a lawn in Guatemala City, Guatemala, I saw a recently fledged Bronzed Cowbird (*Molothrus aeneus*) following and begging food from a Rufous-collared Sparrow (*Zonotrichia capensis*). I watched them intermittently for about 1 h during which time the sparrow fed the cowbird frequently. Once the cowbird flew to the ridge of a low roof, followed by the sparrow carrying food, which it gave to the young bird. This sparrow is heavily parasitized by the Shiny Cowbird (*M. bonariensis*) in South America (Friedmann, H., et al., Smithson. Contri. Zool., No. 235, 1977) but there are no records of parasitism of *Z. capensis* by *M. aeneus*.—AMANDA VILLEDA, *8_a Av. 17–32, Zona 1, Guatemala, Guatemala. Accepted 6 Nov. 1978.*

Wilson Bull., 91(4), 1979, pp. 628–629

Probable Canada Goose × White-fronted Goose hybrids.—Records of hybrid geese produced in captivity are common, particularly within genera (Gray, Bird Hybrids. Tech. Comm. No. 13, Commonwealth Agric. Bureau, Farnham Royal, Bucks, England, 1958; Cockrum, Wilson Bull. 64:140–159, 1952). Davis (Auk 62:636, 1945) and Nelson (Auk 69:425–428, 1952) each reported single instances of Canada Goose (*Branta canadensis*) × Lesser Snow Goose (*Anser caerulescens caerulescens*) hybrids in captivity and Bailey (Auk 66:197, 1949) recorded a similar hybrid in the wild. Thirty *B. canadensis* × *A. c. caerulescens* hybrids were observed in the wild by Prevett and MacInnes (Condor 75:124–125, 1973).

Reports of crosses between Canada Geese and White-fronted Geese (*Anser albifrons*) are less common. A captive *B. canadensis* male and a captive female *A. albifrons* produced hybrid offspring that were smaller than the *B. canadensis*, but no plumage description was given (Gray, op. cit.). Cockrum (op. cit.) reported 1 cross and cited Baird ([Note on hybrid goose.] Forest and Stream 2:5, 1873) as reporting another, but again no physical descriptions of the hybrids were presented. Johnsgard (Condor 62:25–33, 1960) reported such crosses in captivity and from the wild.

White-fronted Geese generally migrate west of the Mississippi River (Bellrose, Stackpole Books, Harrisburg, Pennsylvania, 1976), and they are uncommon in Wisconsin. During 4 years of behavioral observations on wild color-marked *B. canadensis* in Wisconsin, the senior author has observed 15 *A. albifrons*. The latter were observed on 3 of 400 days of field activity. In contrast, *B. canadensis* were encountered on every day of fieldwork. When present in the same area, *B. canadensis* and *A. albifrons* often forage together (Johnsgard, Indiana Univ. Press, Bloomington, Indiana, 1975).

On 23 September 1977, while using a 15–60× spotting scope to observe a flock of *B. canadensis* on Horicon National Wildlife Refuge, the senior author noticed 1 adult *A. albifrons* moving with 3 aberrant geese. The 4 geese were grazing with approximately 1000 *B. canadensis* in a dense stand of moist soil plants (*Bidens* spp., *Polygonum* spp., *Carex* spp., and *Cyperus* spp.) for approximately 5 min before they were flushed by passing automobiles.

The 3 aberrant geese appeared identical in size and plumage, having the distinct white face patch of an *A. albifrons* and black neck, bill, and head of a *B. canadensis*. Cheek patches were also present but were indistinct and charcoal gray. A few scattered white feathers were visible on the crown. Body feathers were darker than those of an average *B. canadensis*, but the pattern was similar. The dense vegetation precluded determination of leg and tail color. The senior author observed many of the plumage variations summarized by Hanson (Auk 66:164–171, 1949) while banding more than 10,000 *B. canadensis* on and near Horicon NWR, but none resembled these aberrant birds.

When disturbed by the passing automobiles, 1 *A. albifrons*, the 3 aberrant birds, and 1 previously unnoticed *B. canadensis* took flight. The 5 geese were still together when they disappeared from view (the *A. albifrons* leading and the *B. canadensis* in the rear). The flight behavior, the low probability of observing 3 identical but unusual variants of *B. canadensis* together, and the white face patch of the aberrant geese, support the conclusion that the 5 geese were a family group composed of an *A. albifrons* paired with a *B. canadensis* and 3 hybrid offspring—perhaps yearlings as suggested by the white face patch.

On 23 December 1977, about 14:00 CST, the junior author observed 2 (or possibly more) hybrids of *A. albifrons* × *B. canadensis*, that matched the senior author's description at Lake Newton near Bogota, Jasper Co., Illinois, ca. 484 km due south of Horicon Marsh. On that occasion, the hybrids accompanied 900–1000 *B. canadensis*, 2 *A. albifrons*, and at least 3 *A. caerulescens* as well as other waterfowl. This assemblage was observed for about 10 min from a distance of about 400 m with the aid of a 20× scope.

It is possible that the hybrids noted were the same individuals observed at 2 widely separated points along their migration corridor. Although incomplete, these observations provide plumage descriptions for previously undescribed wild hybrids.—SCOTT R. CRAVEN, *Dept. Wildlife Ecology, Univ. Wisconsin, Madison, Wisconsin 53706* AND RONALD L. WESTEMEIER, *Illinois Natural History Survey, 304 Poplar Dr., Effingham, Illinois 62401.* *Accepted 2 Jan. 1979.*

Wilson Bull., 91(4), 1979, pp. 630–631

Great Blue Herons foraging for small mammals.—Although there are numerous reports of Great Blue Herons (*Ardea herodias*) feeding on small mammals (e.g., Bent, U.S. Natl. Mus. Bull. 135, 1926; Palmer, Handbook of North American Birds, Yale Univ. Press, New Haven, Conn., 1962), most are single observations that provide little indication that Great Blue Herons may specialize on such prey. The best documentation of small mammals in the diet of herons was reported for the closely related Grey Heron (*Ardea cinerea*) (Hibber-Ware, Ibis 82:433–450, 1940; Lowe, The Heron, Collins, London, 1954; Owen, Proc. Zool. Soc. London 133:597–617, 1960; Milstein, Ardea 58:171–257, 1970). This note reports the occurrence of small mammals in the diet, describes terrestrial foraging behavior and reports 3 new prey species of the Great Blue Heron.

During a study of Great Blue Heron movement patterns and feeding behavior in central Minnesota, 7 April to 22 July 1977, I made daily observations, totaling 430 h, on the feeding behavior of 4 male radio-tagged herons. All radio-tagged herons carried dorsal wing streamers which allowed reliable identification. Each marked bird defended at least 1 permanent foraging area away from the nesting colony during the study period. Approximate individual estimates of the length of actively defended shoreline are as follows: bird A-01 = 0.60 km, A-77 = 1.37 km, T-11 = 0.86 km, K-50 = 1.10 km ($\bar{x}$ = 0.98 km). Feeding territories ranged from 13.7–34.1 km from the colony, and only intraspecific territorial encounters were observed on these areas. Based on the daily observations throughout the study, 2 herons were piscivorous (K-50 and T-11), while the other 2 birds (A-77 and A-01) had a mixed diet that included many species of small mammals (Table 1). The apparent absence of mammals in the diet of K-50 and T-11 may have resulted from the inaccessibility of their foraging areas. I was only able to observe them for 42.5 and 56.5 h, respectively.

From 15 May to 12 June, during 20.5 h of observation, bird A-77 maintained an aquatic feeding territory 13.7 km from the colony. Prey observed captured on this territory included only black bullhead (*Ictalurus melas*) and sunfish (*Lepomis* sp.). On 13 June A-77 had estab-

TABLE 1

TYPE AND NUMBER OF PREY OBSERVED CAPTURED BY RADIO-TAGGED GREAT BLUE HERONS, 7 APRIL TO 22 JULY 1977

	Individual herons			
Prey	K-50	T-11	A-77	A-01
Bullhead (*Ictalurus melas*)	50+	25+	100+	25+
Sunfish (*Lepomis* sp.)	2	5	3	—
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	—	—	28	8
Eastern chipmunk (*Tamias striatus*)*	—	—	3	2
Prairie pocket gopher (*Geomys bursarius*)	—	—	1	4
Eastern fox squirrel (*Sciurus niger*)*,[a]	—	—	—	1
Eastern cottontail (*Sylvilagus floridanus*)*,[a]	—	—	—	1
Leopard frog (*Rana pipiens*)	—	—	—	8
Grasshoppers (unidentified spp.)	—	—	—	10+

* Species not previously reported as prey of Great Blue Heron.

[a] Juvenile.

lished a new feeding territory 20.5 km from the colony. In 83.0 h of observation, from 13 June to 6 July, A-77 appeared to restrict its foraging to the uplands. During this period I observed it capturing thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) almost exclusively. Terrestrial foraging occurred in lake cabin yards, a gravel pit, along the shoulder of a gravel access road and in alfalfa fields. From 7–21 July, during 78.5 h, A-77 foraged in both aquatic and terrestrial areas. I saw A-77 capture 32 small mammals from 13 June to 21 July in 161.5 h of observation.

During 85.5 h from 29 June to 22 July, bird A-01 was observed foraging only in upland areas adjacent to a small pond 20.1 km from the colony. These foraging areas included corn and alfalfa fields, upland hardwood forests, and dry roadside ditches. During this period 16 small mammals were captured, including 3 species not previously reported as prey of Great Blue Herons: eastern chipmunk (*Tamias striatus*), eastern fox squirrel (*Sciurus niger*) and eastern cottontail (*Sylvilagus floridanus*). In contrast, from 16 April to 28 June, during 63.5 h of observation, I saw this heron feed only in aquatic areas, ranging from 4–23 km from the colony. I saw only black bullheads captured in these areas.

Terrestrial foraging consisted of 3 different series of behaviors. (1) Searching for prey consisted of a "slow walk" comparable to the "Walk Slowly" described by Meyerreicks (Nuttall Ornithol. Club No. 2, 1960) except that the neck was held in a more vertical outstretched position, with the bill pointed upward 40–60° from the horizontal. (2) Movement toward prey was extremely slow (it sometimes took over 2 min to walk fewer than 10 m) and can best be described as a "slow stalk." The birds would often stop in mid-stride and maintain that position for more than 2 min before resuming movement. The most conspicuous component of the stalk was the head and neck swaying from side to side. (3) When 2–3 m from the prey, the heron gradually lowered its neck and oriented its bill directly toward the prey. Prior to striking, the head moved toward the base of the neck. A body lunge always accompanied the "Bill Thrust" (Kushlan, Nat. Audubon Soc. Res. Rep. No. 7, 1978).

All herons observed capturing prey used their mandibles to grasp, rather than spear or stab prey. Of the 48 mammals captured by the 2 marked birds, 45 were carried to water, dipped and swallowed head-first.—R. W. PEIFER, *Gen. Biol. Prog., Univ. of Minn., Minneapolis, Minnesota 55455. Accepted 10 Feb. 1979.*

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ORNITHOLOGICAL LITERATURE

BEHAVIOURAL ECOLOGY: AN EVOLUTIONARY APPROACH. By John R. Krebs and Nicholas B. Davies (eds.). Sinauer Assoc., Sunderland, Mass., 1978: xi + 494 pp., 86 numbered figures, 11 tables. $34.00 cloth, $18.50 paper.—Among a number of recent, similarly titled syntheses of ecology and behavior, this book stands as a novel and stimulating exception. Normally, such books either follow textbook format or consist of separately authored, at best loosely related papers stapled together and given a single, all encompassing title. Krebs and Davies offer a successful innovation based on the latter approach. The resulting book is both an up-to-date summary of research in a rapidly expanding field of ecology, and a warehouse of new, as yet little-tested ideas and fields of exploration.

The book contains 14 review papers by as many authors, all but 3 from British universities. The papers are grouped into 3 somewhat artificial categories, each with an introduction by the editors, dealing with (1) predatory and anti-predatory strategies, (2) sex, mating, and communication, and (3) environmental and reproductive life-history strategies. The writing and carefully cross-referenced editing are aimed at providing serious, upper level students of behavior with succinct summaries of "areas in which ethology, ecology, and the theory of natural selection have come together in the last few years to create new and stimulating ideas" (p. ix, preface). A distinctly theoretical perspective underlies and unites every paper, although little formal mathematics is used or required of the reader. Most of the reviews concentrate on examining experimental or field data that demonstrate and test certain theoretical ideas. As such, the book cannot and should not replace more general textbooks that outline basic concepts of behavior and ecology. Many areas of animal behavior are not covered, including learning, navigation and locomotion, migration, coevolution, and communication (beyond the abstract, theoretical level in Ch. 10). Rather, the topical nature of the individual chapters introduces the student, primarily through examples, to hypothesis testing and to a set of modern concepts regarding strategic optimization in time and energy allocation, social organization, reproductive output, and the use of space. Because many of these concepts are still in the midst of being tested and formalized, an air of excitement pervades the writing in virtually every chapter. Fresh approaches and some new, original data make the book as valuable to the seasoned professional as it is to the student.

The text is abundantly cross referenced, providing continuity between different chapters that use similar concepts. Among the recurring themes are optimal foraging theory, kin selection, sexual selection, and Maynard Smith's widely cited "evolutionarily stable strategy" (ESS). Nearly 900 literature references are grouped in the back, and following each entry is a list of locations in the text where the work is cited. This useful feature makes the book an encyclopedic reference text even for the casual user. As a measure of the recent explosion of work in this field, the median year of publication in this vast list of references is 1973. Complete subject and organism indexes are also provided.

The editors open with a general chapter outlining concepts and approaches used repeatedly in the book, paying particular homage to advances made by D. Lack, J. H. Crook, and R. H. MacArthur. Above all, they emphasize the revolutionary contribution to social theory made by W. D. Hamilton, whose treatise on kin selection "provide(s) a genetical framework for interpretting all social behaviour. His idea underlies the thinking on almost every page of this book" (p. 14). This slight overstatement—echoing the thesis of Dawkins' *The Selfish Gene*—accurately demonstrates the academic biases of most of the book's authors.

Certain chapters will be of particular interest to researchers in avian behavioral ecology. Krebs (Ch. 2) gives an excellent review of experimental and field tests of optimal foraging strategies, analyzed from the perspective of how predators should—and apparently do—make decisions regarding where to forage and what prey to eat. B. C. R. Bertram (Ch. 3) and S. T. Emlen (Ch. 9) review the theoretical advantages to group-living in vertebrates. Bertram approaches the question primarily in terms of finding prey and avoiding predators. Emlen reviews cooperative breeding in birds, emphasizing 3 very different case histories (Florida Scrub Jays [*Aphelocoma coerulescens*], Groove-billed Anis [*Crotophaga sulcirostris*], and White-fronted Bee-eaters [*Merops bulockoides*]) where good field data are available. His review is more successful at precisely stating some of the appropriate cost-benefit questions, and listing the possible answers, than it is at providing direct answers for this complex problem. The reason for this lack of resolution—perhaps more acute here than in other chapters—is best explained by his concluding remark (p. 281) that "studies of cooperative behaviour remain in their infancy." Ecological factors pertaining to sex (Ch. 6) and sexual selection in the broad sense (Ch. 7) are discussed by J. Maynard Smith and T. R. Halliday, respectively. Both articles are well written reviews of recent advances in ancient controversies, and provide 2 of the book's best examples of where field analyses, even though extensive, still fall far short of theoretical work in their field. Dawkins and Krebs (Ch. 10) provide an innovative interlude with an essay questioning the classical perspective with which animal communication has been studied up to now. Building upon the "selfish gene" approach, they hold that animal signals are better viewed as selfish, manipulative devices, than as accurate displays of information or internal states. This "cynical" view of interactions between individuals directly contradicts classical ethological approaches, and is bound to stimulate debate in coming years. Davies (Ch. 11) reviews territoriality in birds and mammals, first in terms of its costs and benefits to individuals with differing habits, and, second, as it relates to population regulation. He adopts an extremely loose definition of territory: "whenever individual animals or groups are spaced out more than would be expected from (chance alone)" (p. 317). This definition may have forced Davies to slight his treatment of ecological determinants of territory size in favor of now less controversial questions regarding population regulation and proximate signals used in territorial defense. H. S. Horn (Ch. 14) presents the most easily read paper available that reviews theoretical ideas about life history strategies. Although Horn "personally think(s) that the terms 'r-selection' and 'K-selection' are barbaric" (p. 413), his elegant prose and simple graphical representations concisely explain why this apparent dichotomy between reproductive strategies is real in nature. As Horn (p. 411) correctly points out, "most of the theoretical discussions of tactics of life-history are (so) overloaded with turgid mathematical formalism (that) many of the important papers are unintelligible even to the authors of other important papers." In contrast, Horn's paper is a must for all who seek a brief, non-mathematical and unifying treatment of environmental relationships among body size, reproductive output, longevity and dispersal patterns.

Other chapters are on insect sociality (Heinrich), anti-predator strategies (Harvey and Greenwood), mate-searching strategies in dung-flies (a theoretical chapter with narrow scope, by Parker), habitat selection (spotty review including some circular reasoning, by Partridge), and "optimal behaviour sequences" (some sophisticated, difficult to follow rules for decision-making, by McCleery).

The book is a reasonably priced (in paperback), and highly readable summary of an expanding branch of ecology. In this branch the individual animal is viewed as having evolved into a scheming strategist whose every move, be it minute to minute, season to season, or generation to generation, is governed by an insatiable genetic drive toward selfish optimization. Precisely what is being optimized? Ultimately, the common currency is genetic fitness, which, because it is a *relative* measure, can never really be optimized. Instead, as assumed in this book, animals are pitted against the environment and one another in never-ending games, where the most successful strategist is the one that—by virtue of this success—leaves the greatest genetic contribution to succeeding generations. This is a critical and controversial assumption, and one that can be tested only indirectly at best. It is Darwinism carried toward its logical extreme. Krebs and Davies provide us with a series of reviews that summarize the progress made through 1978 in testing whether behavior conforms to this assumption.—JOHN W. FITZPATRICK.

ORNITHOLOGICAL NEWS

THIRD JOINT COS-WOS MEETING IN 1980

The third joint meeting of The Cooper Ornithological Society and The Wilson Ornithological Society will be held in Corpus Christi, Texas, at the La Quinta Motor Inn from 19–23 March 1980. Paper sessions are scheduled to start the morning of 20 March. The announcement of schedule and arrangements, and a call for papers, will be mailed to members of COS, WOS and AOU using the new Ornithological Societies of America mailing labels. This mailing is scheduled for 1 December 1979. The sponsoring organizations of the meeting are Corpus Christi State University and the Coastal Bend Chapter of the National Audubon Society. Chairpersons of the committees on arrangements and on scientific program are, respectively, Brian R. Chapman, Division of Biology, Corpus Christi State University, Corpus Christi, Texas 78412, and Jerome A. Jackson, Department of Zoology, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

FIFTH PAN-AFRICAN ORNITHOLOGICAL CONGRESS

The Fifth Pan-African Ornithological Congress will be held 23–30 August 1980, in Lilongwe, Malaŵi. The theme is "Current state of knowledge of African birds" (with pointers to future research). Pre- and post-congress excursions are planned to indigenous forests, mountain areas, lake shore, game parks and nature reserves, offering a variety of habitats of ornithological interest within Malaŵi. Registration fees are due 31 March 1980. For applications and further information please contact Len Gillard, Executive Secretary, Fifth Pan-African Ornithological Congress, P.O. Box 84394, Greenside, Johannesburg 2034, South Africa.

SEVENTH WOODCOCK SYMPOSIUM

The Seventh Woodcock Symposium will be held 28–30 October 1980, at University Park, Pennsylvania. The symposium is being co-sponsored by the Pennsylvania State University, the Pennsylvania Game Commission and the U.S. Fish and Wildlife Service. Persons wishing to present papers on any aspect of woodcock research or management should send title and abstract to: Review Committee Chairman Thomas Dwyer, Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service, Laurel, Maryland 20811 (301/776-4880). Abstracts should be limited to 200–250 words and be submitted before 1 March 1980. Papers accepted by the Review Committee will be published in the Symposium Proceedings. Persons considering attending the symposium can obtain future announcements by writing Mr. Dwyer.

PACIFIC SEABIRD GROUP

The Pacific Seabird Group will hold its 6th Annual Meeting 23–26 January 1980, at the Asilomar Conference Grounds, Pacific Grove, California. Scientific paper sessions and "symposia" will be held in one of the most beautiful settings in the west and all persons interested in marine birds are invited to attend and participate. For further information contact Palmer Sekora, Program Chairman, Route 2, Box 208, Corvallis, Oregon 97330.

NORTHEAST ENDANGERED SPECIES CONFERENCE

A symposium on threatened and endangered species in the northeast United States from Virginia to Maine will be held 9–11 May 1980, in Provincetown, Cape Cod, Massachusetts.

EDITOR'S ACKNOWLEDGMENTS

I wish to express my sincere appreciation to referees and authors, without whose assistance and cooperation the difficult job of editing and producing a viable journal would have been impossible. I also acknowledge the editorial staff for a job well done. Volume 91 has been a learning experience for us all. I also thank Mrs. Pat Urquhart, Departmental Secretary, Department of Ornithology, ROM, for doing the impossible job of typing the index.—Jon C. Barlow, *Editor*

NECROLOGY

We are saddened to report that Maurice Broun, a Life Member of The Wilson Ornithological Society, died on 2 October 1979. Mr. Broun is well remembered for his long association with the Hawk Mountain Sanctuary, in Pennsylvania.

INDEX TO VOLUME 91, 1979

By Nancy J. Flood, Gary R. Bortolotti and Peter Thompson

This index includes references to genera, species, authors and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume. Common names are as they appeared in the volume. Reference is made to books reviewed, reviewers and announcements as they appeared in the volume.

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