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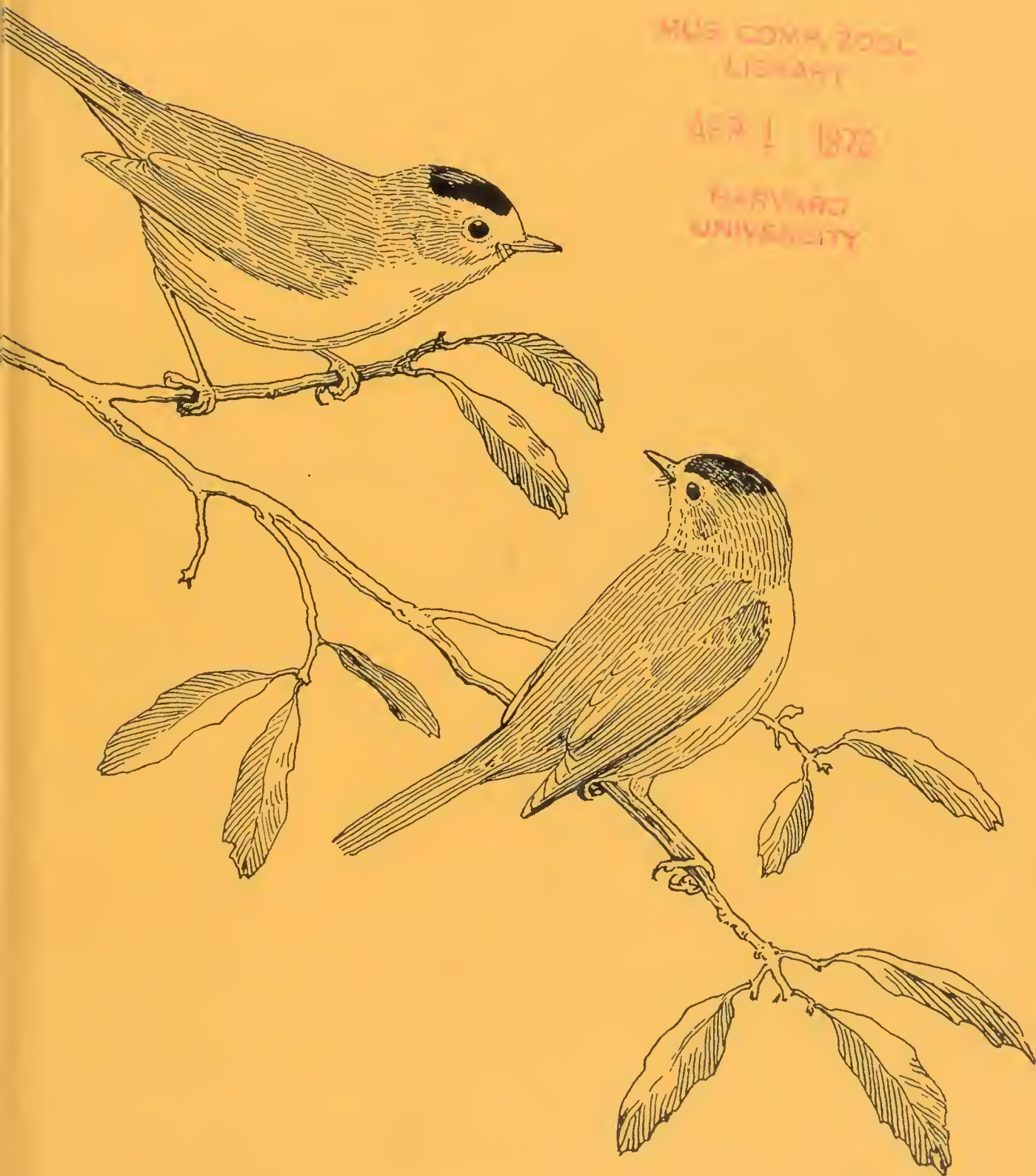
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CONTENTS

- ROSS' GEESE (*CHEN ROSSII*) NESTING ON AN ISLAND AT KARRAK LAKE,
NORTHWEST TERRITORIES, 24 JUNE 1967, Photograph by *John P.
Ryder* Facing Page 5
- A POSSIBLE FACTOR IN THE EVOLUTION OF CLUTCH SIZE IN ROSS' GOOSE
John P. Ryder 5
- OOLOGICAL DATA ON EGG AND BREEDING CHARACTERISTICS OF BROWN
PELICANS *Daniel W. Anderson and Joseph J. Hickey* 14
- NICHE OVERLAP IN FEEDING ASSEMBLAGES OF NEW GUINEA BIRDS
John Terborgh and Jared M. Diamond 29
- AN APPRAISAL OF THE SONG OF THE BLACK-CAPPED CHICKADEE
Keith L. Dixon and Raymond A. Stefanski 53
- STATUS AND SPECIATION IN THE MEXICAN DUCK (*ANAS DIAZI*)
John W. Aldrich and Kenard P. Baer 63
- PARASITISM BY THE BROWN-HEADED COWBIRD ON A BROWN THRASHER
AND A CATBIRD ... *Robert M. Mengel and Marion Anne Jenkinson* 74
- HIGH DENSITY OF BIRDS BREEDING IN A MODIFIED DECIDUOUS FOREST
David W. Johnston 79
- INDEXING POPULATION DENSITIES OF THE CARDINAL WITH TAPE-
RECORDED SONG *Douglas D. Dow* 83
- GENERAL NOTES
- ON THE VALIDITY OF SOME SUPPOSED "FIRST STATE RECORDS" FROM YUCATÁN
Kenneth C. Parkes 92
- HIGH DENSITY MALLARD NESTING ON A SOUTH DAKOTA ISLAND
Rod C. Drewien and Larry F. Fredrickson 95
- COURTSHIP DISPLAY OBSERVED BETWEEN TWO SPECIES OF BUTEOS
Bruce R. Wolhuter and Frank Kish 96
- FOOD HABITS OF WINTERING SPARROW HAWKS IN COSTA RICA *Robert E. Jenkins* 97
- MARSH HAWK CHASES CROWS MOBING OWL *William E. Southern* 98

RUDDY TURNSTONES MAKING USE OF YELLOW-CROWNED NIGHT HERONS FOR FOOD-FINDING	<i>F. Haverschmidt</i>	99
COMMON TERNS PIRATING FISH ON GREAT GULL ISLAND	<i>Helen Hays</i>	99
SAND-KICKING CAMOUFLAGES YOUNG BLACK SKIMMERS	<i>Helen Hays and Grace Donaldson</i>	100
BARN OWLS HUNTING BY DAYLIGHT IN SURINAM	<i>F. Haverschmidt</i>	101
FOOD PREFERENCES OF A HAND-RAISED BLUE JAY	<i>A. R. Weisbrod</i>	101
A WHITE-THROATED SPARROW NEST IN WESTERN PENNSYLVANIA	<i>Ted Grisez</i>	102
ORNITHOLOGICAL NEWS		104
ORNITHOLOGICAL LITERATURE		105
<p>Joseph J. Hickey (Ed.), <i>Peregrine Falcon Populations</i>, reviewed by David B. Peakall; Burt L. Monroe, Jr., <i>A Distributional Survey of the Birds of Honduras</i>, reviewed by Eugene Eisenmann; Edgar M. Reilly, Jr., <i>The Audubon Illustrated Handbook of American Birds</i>, reviewed by Mary Heimerdinger Clench; Kurt M. Bauer and Urs N. Glutz von Blotzheim, <i>Handbuch der Vögel Mitteleuropas</i>, reviewed by Sam E. Weeks.</p>		

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ROSS' GEESE (*Chen rossii*) nesting on an island at Karrak Lake, Northwest Territories, 24 June 1967. Note males standing, females incubating and the paucity of vegetation within the nest territory.

A POSSIBLE FACTOR IN THE EVOLUTION OF CLUTCH SIZE IN ROSS' GOOSE

JOHN P. RYDER

ABOUT 25 years ago David Lack advanced the theory that clutch size, in birds which feed their young, has evolved in relation to the size of the brood producing the greatest number of young that reach sexual maturity, the ultimate limiting factor being the availability of food required by the young (Lack, 1954, 1966*a*). According to another major viewpoint (Wynne-Edwards, 1955, 1962), clutch size has evolved in relation to, and compensates for, the average mortality of a population. This idea, based primarily on the theory of "intergroup" selection, says that clutch size increases in a depleted (low density) population and decreases as the population density increases. Wynne-Edwards (1962) gives many examples of this "density-fecundity" relationship in most animal groups. The ultimate limiting factor in his proposal is food, whereas the proximate limiting factor is the regulation of population density by social behavior.

Arguments for and against both theories are now in the literature (Brown, 1964; Cody, 1966; Lack, 1954, 1965, 1966*a*; Perrins, 1964; Skutch, 1967; Smith, 1964; Wiens, 1966; Wynne-Edwards, 1955, 1962, 1963).

Few ideas have been published on the limitations or on the significance of clutch size in birds which do not feed their young, for example the family Anatidae (ducks, geese, and swans).

The purpose of this paper is to suggest that the clutch size of Ross' Goose (*Chen rossii*), a nearctic anserine, has evolved in relation to the food reserves which the female accumulates before arriving on the breeding grounds. I suggest that an important factor in the evolution of the clutch size is the number and size of eggs which provide enough food reserves for the newly hatched young until they are able to feed themselves (see Kear, 1965), and which also leave enough for the female to give maximum attentiveness to the eggs during incubation. The amount of food the female stores is limited by the total increase in body weight she can carry during the spring migration and maintain long periods of flight.

Lack (1966*b*) published one of the first suggestions concerning the significance of clutch size in waterfowl. He states that the average clutch size for each species has been evolved in relation to both the average availability of food for the female at the time and place of egg laying, modified by the relative size of the egg. He expresses essentially the same idea in a recent, more detailed review of waterfowl clutch sizes (Lack, 1968). My hypothesis

Frontispiece: The larger birds are Lesser Snow Geese (*Chen hyperborea*).



FIG. 1. Ross' Goose nesting island at Karrak Lake, NWT., 25 June 1966.

follows closely that of Lack (1966*b*, 1968) with modification to apply to Arctic nesting geese. It is based on the assumption that the breeding female goose is independent of the food supply at the time and place of egg laying.

Each spring Ross' Geese migrate from their California wintering area in the Sacramento and San Joaquin Valleys to the nesting grounds in the Canadian Arctic, a distance of about 4,000 miles. Most of the population nests on islands in shallow tundra lakes in the Perry River region of the central Arctic (Ryder, 1969) (Fig. 1, 2). Small segments also nest in the Hudson Bay area (Cooch, 1954; Barry and Eisenhart, 1958; MacInnes and Cooch, 1963).

Before and during the spring migration the geese feed extensively and by the time they arrive in the north, their body weights and fat reserves are at a maximum compared to any other time of year. Lack (1966*b*) does not account for this weight increase and large amounts of fat found in Ross' and other Arctic nesting geese at the time of arrival on the nesting grounds (see Hanson, 1962 for Canada Geese (*Branta canadensis*); Barry, 1962 for Brant (*Branta bernicla*); Cooch, 1958 for Blue Geese (*Chen caerulescens*); Barry, 1967 for recent data on the Anderson River, N.W.T. population of Black Brant (*Branta nigricans*), Lesser Snow Geese (*Chen hyperborea*), and White-fronted Geese (*Anser albifrons*); Hanson et al., 1956 for Canada Geese, Lesser Snow Geese and White-fronted Geese from the Perry River region; Macpherson and Manning, 1959 for Canada Geese from Adelaide Peninsula, N.W.T.). Hanson (1965) states that the peak fat reserve in



FIG. 2. Ross' Goose mated pair at Arlone Lake, NWT., July 1964.

Canada Geese at the time of arrival on the nesting grounds in northern Ontario is probably an evolutionary development which insures survival of the adult until spring breakup. This type of reasoning is prevalent in the literature of Arctic goose biology (see above references) and what little data we have indicates that it is most likely true. However, none of the literature suggests that the food reserves of the female goose are of evolutionary significance in allowing her to spend more time on the nest.

During the egg laying period Ross' Geese remain on the nesting islands for long periods, only occasionally visiting the mainland feeding marshes. It is hard to believe that the purpose of these visits to the mainland is to prepare her for the fasting period ahead, especially in late seasons when the vegetation is covered with snow or still frozen in the ground and food is scarce.

Ross' Geese usually lay four eggs (Ryder, 1967). Attentiveness increases with each egg in the clutch and incubation begins after the last egg is laid (Fig. 3). During egg laying and incubation, the breeding female can lose up to 800 grams (44 per cent) of body weight. Of this, about 100 grams are lost by ovary regression. During incubation she leaves the nest for short periods to obtain what little food is available near the nest site and rarely will she, accompanied by the male, fly to the mainland marshes to feed. It appears that throughout the incubation period the female is relying heavily on food reserves stored before the nesting season. It is also apparent that the short pre-egg stage and egg laying period (about 10 days) are too short to allow enough food intake to last through the 22-day incubation



FIG. 3. Ross' Goose nest on island at Karrak Lake, NWT., 13 June 1966.

period, even with occasional supplementary feedings. Hanson (1962) states that the resistance to fasting is frequently associated with the nutritive condition at the start of the fast. In Arctic geese this resistance is likely acquired before arrival on the nesting grounds.

The hatching time for a Ross' Goose clutch of three or four eggs is one or rarely more than two days. The goslings and adults leave the nest site within a few hours and begin the post-nuptial period during which the family spends most of its time feeding and later the adults complete the annual molt. Although some body weight is lost during the molt (Ryder, 1967), it is regained before the southward migration in late August and early September.

I propose that the differential utilization of stored food during the nesting season has been most important in the evolution of the clutch size in Ross' and other Arctic nesting geese. Figure 4 presents three possible "cases" which attempt to explain graphically the mechanisms by which present clutch size may have arisen.

Case 1 depicts a situation in which the female, with enough food reserves in her body, is able to maintain attentiveness to the eggs throughout the entire incubation period. Concurrently, the ova are supplied with a sufficient food reserve for the young until they are able to feed themselves. The total reserve allocated to the female and to the eggs is limited by the amount stored before the breeding season. The number of mature ova is limited so that the female can give maximum protection to the clutch. Case 1 proposes that the female is independent of a food supply at the time and place of nesting. Breeding biology studies of Ross' Geese and other Arctic nesting

geese suggest to me that average clutch sizes have been evolved in relation to the conditions outlined for Case 1.

Case 2 shows that although the total increase in body weight has remained the same, the allocation of food reserves has been decreased to ova and increased to non-ovarian tissues. The direct result here is a smaller reproductive output and an overabundance of food reserve for the female. One obvious "advantage" of this case is that it allows for greater attentiveness to a smaller clutch and increased survival of young. A number of factors might decrease the frequency of this case occurring in a natural population. Firstly, there is no need for the female to retain a food reserve for the post-hatching stage. During this stage, food is abundant in the Arctic, and food storage is not generally considered to be a limiting factor. Secondly, the excess food reserve could have been allotted to the young, by increasing the amount of yolk and size of the egg, to further increase their chances of survival until they are able to feed on their own. Thirdly, low natality added to annual mortality may eventually result in a depletion of the population below recuperable levels, and fourthly, Case 2 favors increased survival of the adult, by supplying more food than is required, and a lowered reproductive output, which is incompatible with the theory of natural selection. Mayr (1963) reminds us that "reproductive success rather than survival [of the adult] is stressed in the modern definition of natural selection." I suggest that Case 2 is rare in natural populations and may be found in two situations: where young geese, breeding for the first time, possibly lay smaller than average clutches (Delacour, 1964); and where a late season in the Arctic delays exposure of nesting habitat. This latter situation forces the female to use some of her reserves while waiting to start nesting. By the time of nest initiation, her reserve is decreased and to give maximum protection to the eggs, allocation to the ova has to be decreased. Smaller clutches in late starting Arctic seasons have been observed in Blue Geese, Brant, Black Brant, and White-fronted Geese (Cooch, 1958; Barry, 1962 and 1967). Atresia of the ovary and resorption of (the contents of) the ova release food reserves to the breeding female.

Case 3 depicts a situation where the number of mature ova is increased in relation to the total increase in body weight. This allows for a larger reproductive output but reduced food reserve for the breeding female. Under these conditions, the females' food storage may be depleted before the eggs hatch, forcing her to leave the nest to feed, allowing for increased exposure of the eggs to weather and predation. The direct result would be high embryo and nestling mortality. Case 3 applies in situations where larger than average clutches are laid. Various workers have reported increased nest and egg loss in such instances (Williams and Marshall, 1938; Hanson and Browning, 1959:

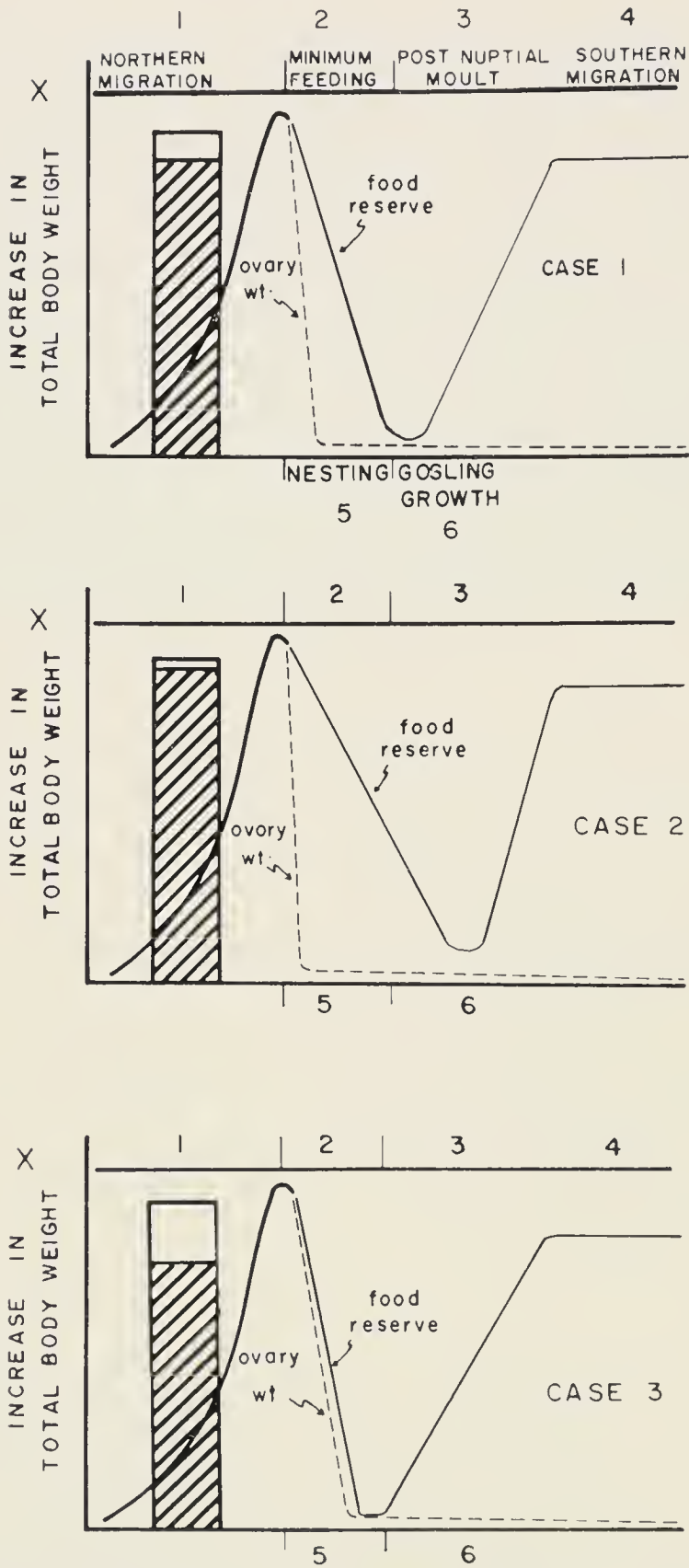


FIG. 4. Proposed mechanism for the evolution of clutch size in Ross' Goose. The vertical bar represents the proportion of spring food reserves acquired by the breeding female before arrival on the nesting grounds, which are allotted to non-ovarian (hatch

Cooch, 1961; Hilden, 1964; Perrins, 1964; Barry, 1967). Poor success of large clutches is attributed to incubation difficulties, possible discomfort to the female resulting in her moving the eggs from the nest; eggs accidentally rolling out the nest when she changes position (Delacour, 1964), and increased breakage when the eggs are layered in the nest, a situation I found common in large clutches of Ross' Geese. Cooch (1961) noted that the larger clutches of Blue Geese take longer to hatch than those of average size and that the individuals which hatch last are weak, often unable to keep up to the older members of the brood. The "prognosis of survival for such goslings is poor." Hilden (1964) points out that in large broods of *Aythya* in Finland, the hen experiences difficulties keeping the brood intact when threatened by an enemy and when brooding in cold weather. This results in increased brood mortality. Eygenraam (1957) cited in Hilden (1964) showed that the largest broods of the Mallard (*Anas platyrhynchos*) are reduced at a relatively faster rate than those of normal size. In Arctic nesting geese, the larger clutch, in addition to presenting the problems outlined above, take longer to complete development. Time to complete the reproductive cycle is short in the Arctic (see Cooch, 1961; Ryder, 1967) and any individual that takes excessive time fails to rear offspring. Late seasons can have the same effect on large broods in terms of development of young. Barry (1962) found 21 young Brant frozen in the ice in the spring of 1957. These geese had hatched in the late season of 1956 and were in perfect shape except that feather development was four to five days short of allowing them to fly.

More intense studies of embryonic, nestling, and fledgling mortality in relation to clutch size are required for most species before definitive statements are made regarding the credibility of Case 3. The investigations of Cooch (1958) on Blue Geese and the reviews of long term studies in Lack (1966a) strongly support the contention that larger than average clutches do not necessarily produce the greatest number of young which survive to sexual maturity. I suggest that Case 3, although existing in current populations of Arctic nesting geese, contributes less than Case 1 to the natural rate of increase of a population.

The mechanisms I have presented to explain the evolution of clutch size in Arctic nesting geese are, for the most part, speculative. I hope that in the future, collection of breeding biology data from the Anatidae and other groups which do not feed their young, will illustrate the validity of the ideas expressed in this paper.

lines) and ovarian tissues. The horizontal X-line represents the weight above which the female cannot sustain long periods of flight during the spring migration. Weights are relative but nesting season phenology is based on data collected during the 1963 and 1964 nesting seasons (Ryder, 1967). See text for further explanation.

SUMMARY

Three possible cases or alternatives are presented to explain the evolution of clutch size in Ross' Geese and other Arctic nesting geese, which do not feed their young. It is suggested that food reserves, acquired by the breeding female geese before the time and place of nesting, are allotted to ova and non-ovarian tissues. The number and size of eggs is limited to provide enough reserve food material to the young until they are able to feed themselves, and also to provide the breeding female with food so that she can give maximum protection to the clutch. The total amount of food stored before the breeding season, is limited by the maximum increase in body weight the female can carry during the spring migration.

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OOLOGICAL DATA ON EGG AND BREEDING CHARACTERISTICS OF BROWN PELICANS

DANIEL W. ANDERSON AND JOSEPH J. HICKEY

THE Gulf Coast population of the Brown Pelican (*Pelecanus occidentalis*) is now considered to be endangered by the AOU Committee on Conservation (1968). The circumstances surrounding its decline are not clear. Murphy (1936:102, 808-822) suggested that some breeding populations of Brown Pelicans "normally" fluctuate in response to fluctuating food supplies in relation to such factors as Humboldt Current changes, as well as other factors. Conney (1967), Kupfer (1967), Peakall (1967), Risebrough et al. (1968), and Wurster (1969) have explained some potential physiological effects of chlorinated-hydrocarbon and related environmental pollutants on mammalian and avian reproduction, which might apply, as well.

This paper presents information, obtained from major oological collections in North America, regarding some egg and reproductive parameters of the Brown Pelican. Ratcliffe (1967) and Hickey and Anderson (1968) have utilized oological sources to document changes in shell thickness and shell weight among seven species of birds. These changes were related to (1) the widespread introduction of persisting chlorinated hydrocarbons into the environment and (2) reproductive failures associated with shell-breakage and loss.

The lack of field data regarding certain breeding and egg characteristics from prior to and possibly during the decline of the Brown Pelican necessitated our attempt to glean whatever information possible from museum and private-egg collections. An understanding of the present situation, in addition, requires an evaluation of the geographical and temporal variations in the characters of interest.

METHODS

Measurements.—Eggs were weighed to the nearest 0.01 gram (g) on a torsion balance. Improper cleaning undoubtedly influences shell-weight and possibly also shell-thickness measurements. We used four criteria to determine if eggs had been properly blown: (1) a tendency to settle to one side when rolled on a smooth surface, (2) loose contents, (3) roughness on the interior of the shell, and (4) visual examination. In the course of measuring over 34,000 eggs of 25 species, we found about 200-300 broken or cracked eggs and a larger number with large holes. These lent themselves to close examination, and all proved to be satisfactorily cleaned. Eggs with holes larger than 7 mm were either not measured, or their weights were corrected to those with a 3-mm hole. This was accomplished by taking a small piece of shell, weighing it, and visually "filling" the hole. Egg lengths and breadths were measured to the nearest 0.01 centimeter with a standard, precision vernier caliper. Egg shapes were determined by comparison with the shapes

TABLE 1

CLUTCH SIZES AND INCUBATION STAGES OF EGGS TAKEN BY OOLOGISTS PRIOR TO 1943

Est. Stage of Incubation	Incubation Rating	Sample Size	Mean Clutch Size	95% C. L.
First egg-3 days ¹	1	72	2.94	0.32
4-12 days	2	137	2.93	0.31
13-21 days	3	27	3.07	0.50
22-30 days	4	0	—	—
All combined	—	236	2.95	0.27

¹ This stage represents a period of approximately 9 days.

described by Palmer (1962:13) and Preston (1968). Shell thickness was measured to the nearest 0.01 mm with a specially adapted micrometer, the procedure being described by Hickey and Anderson (1968). Thickness included shell and associated membranes at the girth of each egg.

Information from Data Slips.—Data slips, giving species, date of collection, stage of incubation, location, collector, and other pertinent information accompanied each set of eggs we measured. Due to the inadequacy of incubation terminology and the inability to identify incubation stage accurately (Storer, 1930), mean dates of set-collection (corrected on the basis of reported incubation to give date of clutch completion) can only provide an estimate of breeding phenology. The dates together for an area really only represent a mean over the years, but do suggest general trends and provide an index to length and variability of breeding season from region to region. We felt that oologists' estimates of incubation could, at best, only be categorized to the nearest one-fourth of the period from first egg to the end of incubation. The incubation period of the Brown Pelican is not precisely known (Palmer, 1962:277). We have used Mason's (1945) estimate of about 30 days for our calculations here and have estimated the mean number of days that our samples were incubated on the basis of our four incubation categories (Table 1, col. 1). In our series of samples, mean stage of incubation in days subtracted from mean date of set-collection provided an estimate of date of clutch completion. Unincubated ("fresh") eggs were included in the analysis of clutch size, after testing to determine if fresh sets might be biased by the collection of incomplete clutches. When sets of fresh eggs were separately compared with those of later incubation (*t*-test), no significant differences in clutch size were found ($P > 0.05$, Table 1). There remains the possibility that some egg collectors sought larger clutches.

Calculations and Indices.—All data were analyzed with an IBM 1620 computer. Statistical analyses followed Steel and Torrie (1960). A size index for eggs was calculated by multiplying length by breadth and was used as a crude index to volume. In a study of White Pelicans (*P. erythrorhynchos*) (D. W. Anderson and J. J. Hickey, unpublished), we have found displaced volume to be correlated with this size index ($P < 0.001$).

Geographical variations in egg size, shell thickness, shell weight, clutch size, and egg dates were determined in a stepwise manner as follows: (1) current subspecific range boundaries were determined from the AOU Check-list (1957) and Palmer (1962:275), and the range was then subdivided into small geographic units such as a single state; (2) the eggshell data for these were then tested for significant differences and regrouped until a region was obtained containing a maximum number of subunits that were not significantly different from each other; (3) groupings never included more than one

TABLE 2
GEOGRAPHICAL VARIATION IN EGGSHELLS OF NORTH AMERICAN BROWN PELICANS,
1879 TO 1943¹

Subspecies Area	occ West Indies	car S.C.	car Fla., Ga.	car La.	car Panama	car Texas	cal Baja Calif.	cal So. Calif.
Number	6	43	208	42	7	115	174	85
Wt. (g)	8.05	9.46	9.78	9.87	9.94	10.00	10.99	10.59
±95% C.L.	±0.90	±0.35	±0.12	±0.32	±0.49	±0.26	±0.18	±0.24
Size Index (cm ²)	33.2	37.6	37.6	38.2	37.4	38.5	40.0	39.0
±95% C.L.	±0.6	±0.9	±0.3	±0.7	±1.0	±0.6	±0.4	±0.7
No. Subelliptical	3	21	109	20	2	52	94	44
No. Oval	3	22	99	22	5	63	80	41
Thickness Index ²	2.42	2.52	2.60	2.58	2.66	2.59	2.74	2.71
±95% C.L.	±0.24	±0.06	±0.02	±0.06	±0.10	±0.04	±0.02	±0.04
Number	6	23	172	24	—	43	83	28
Thickness (mm)	0.510	0.557	0.557	0.554	—	0.557	0.569	0.579
±95% C.L.	±0.031	±0.021	±0.004	±0.014	—	±0.012	±0.008	±0.014

¹ The pre-1943 means that were not significantly different at the 95% level in Duncan's New Multiple Range Test (Steel and Torrie, 1960:107-109, 114) are underscored.

² From Ratcliffe (1967): Thickness index = $10 \times \text{wt. in g} / (\text{length} \times \text{breadth in cm})$.

described subspecies; and (4) phenological subdivisions were kept at the smaller units without regrouping.

RESULTS AND DISCUSSION

Geographical Variation in Egg Parameters.—Egg-size index, shell weight, and shell thickness (Table 2) tended to vary with the size of the bird as discussed by Romanoff and Romanoff (1949:150). Our index to body size was obtained by using two common standard measurements that tend to measure skeletal size (tarsus and culmen) (Fig. 1). These skeletal measurements were taken from Wetmore (1945) and represent those of female birds. Wetmore (1945) ranked the size of the three North American subspecies, from largest to smallest as follows: *P. o. californicus*, *P. o. carolinensis*, and *P. o. occidentalis*.

The general shape categories (Table 2) were, nonetheless, not significantly different ($P > 0.05$, Chi-square test) from area to area or between subspecies. Ordinary shape changes in the eggs of domestic poultry have already been shown to have little effect on the shell present as a percentage of total egg weight (Asmundson and Baker, 1940).

Of the subspecies *carolinensis*, birds from Texas tended to have the largest

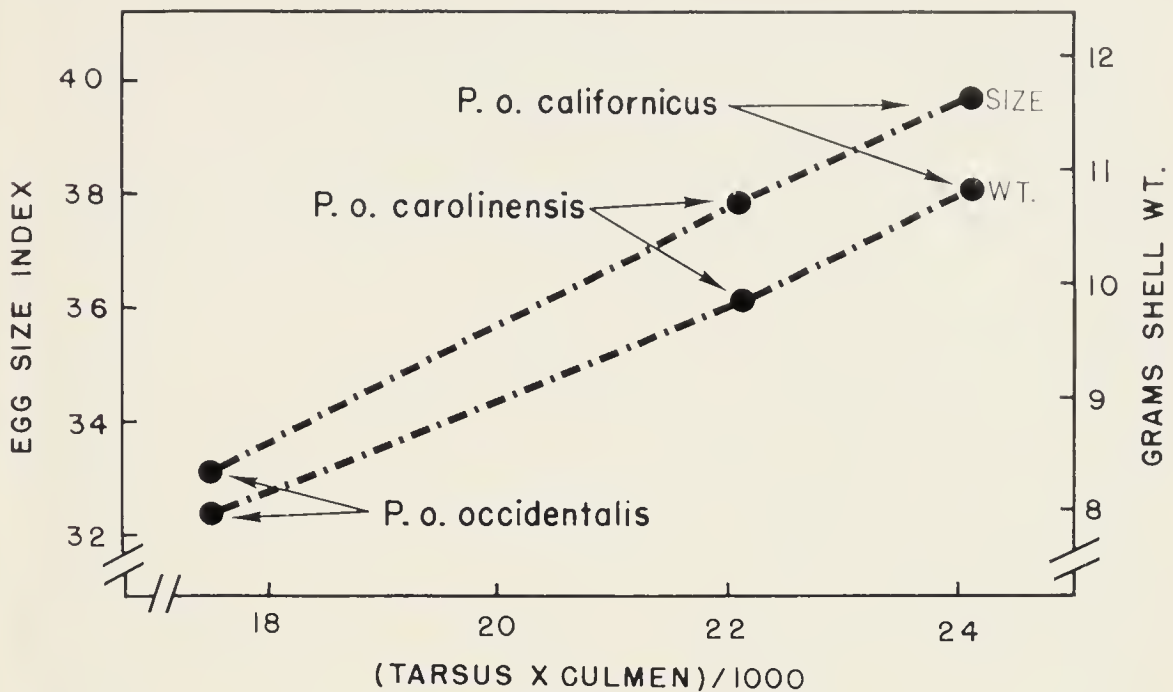


FIG. 1. Relationship between two egg measurements and index to body size in three subspecies of Brown Pelicans. The index to body size was calculated in mm^2 units and is shown on the abscissa. Eggshell size was taken as the product of length and breadth in cm^2 .

eggs. Louisiana eggs tended to be intermediate between those from Texas and those from areas to the east (Table 2). South Carolina birds tended to have smaller and lighter-shelled eggs than birds from farther south in Florida and Georgia, although not significantly so (Table 2). The Baja California eggs (*P. o. californicus*) were represented mostly by specimens from Los Coronados Island but suggested a similar gradient, with egg size decreasing from southern to northern colonies. Lack (1968:279) mentioned this trend among certain congenics in certain tropical Procellariiformes. A continuum in egg size and shell weight between different populations from different areas was suggested in our specimens, especially in *carolinensis*, although shell thickness in the various subspecies seemed relatively stable. Whether or not the intraspecific tendencies are genetic is unknown. They are likely genetic, but standard measurements from museum skins are needed for further comparisons. The interspecific variations in egg size are most likely representative of body size (Fig. 1).

If one assumes that egg size provides an index to body size, the large Texas birds may represent an intermediate between *californicus* and *carolinensis*. Brown Pelicans along the Pacific Coast (*californicus*) have the larger and thicker-shelled eggs (Table 2). Asmundson et al. (1943) showed that larger eggs in several species tended to have the thicker shells, but the essentially

equal thicknesses from all our Gulf and Atlantic Coast eggs suggested that this relationship was not present on an intraspecific basis. The small sample of eggs from Panama suggested that these eggs were most similar to the subspecies *carolinensis*, as Wetmore (1945) has shown with museum skins. Unfortunately, we were unable to obtain egg measurements from Ecuadorian or Peruvian Brown Pelicans. Murphy (1936:820) reported that the Peruvian pelicans are very large and we suspect that their eggs would also be larger and thicker-shelled.

The ecological significance of egg-size difference within a species is largely a matter of speculation. Lack (1966:7) suggests that egg-size differences between different species (and larger groups) are mainly a matter of heredity. The differences we observed on an interspecific basis in Brown Pelicans at least implied that these eggs are represented by relatively distinct gene-pools. Perhaps such gene-pools are even distinct on an intraspecific basis. Mason (1945) showed that Florida Brown Pelican movements, at least, are somewhat restricted under normal circumstances, suggesting potential isolation between breeding groups. Welty (1962:408 quoting Murphy, 1936) also suggests that this species is potentially sensitive to isolating barriers.

Possible Factors for Bias.—It is not our primary objective here to speculate on taxonomic relationships on the basis of eggs; nonetheless, the variations in eggs are expected to relate in some ways to taxonomic characters (Tyler, 1964, 1965). Our interest is mainly to examine natural variation in order to better understand if unnatural change has occurred.

Egg size and shell thickness and composition are known to vary with heredity, age, adult physiological condition, diet, and chemical influence (Romanoff and Romanoff, 1949:152–157, 359; Preston, 1958; Sturkie, 1965: 464, 487–488; Simkiss, 1967:157–197). Shell thickness also varies in different areas of the egg of a given species, the most notable examples probably being the rock-nesting murre (*Uria* sp.) and other seabirds, where thickness tends to increase at the most vulnerable parts (Tuck, 1960:25). Some interspecific differences in thickness have been shown to be related to the hazards associated with placement on different nesting substrates (Belopol'skii, 1957: 133–134). Fortunately, egg collectors drilled their specimens at the girths, the most uniform area for most species (Romanoff and Romanoff, 1949: 157–158).

Shell calcium (about 5 per cent) is utilized, as well, by developing embryos (Simkiss, 1967:198–213); hence, shell weight and also possibly thickness may be biased low if eggs of late-stage incubation are used in the shell-thickness or weight comparisons. Data combined into *carolinensis* and *californicus* categories indicated this trend (Table 3), although not significant statistically (*t*-test, $P > 0.05$) and only amounting to a small percentage

TABLE 3
SHELL WEIGHTS OF PRE-1943 EGGS OF TWO SUBSPECIES OF BROWN PELICAN
AT DIFFERENT INCUBATION STAGES

Subspecies Incubation Stage	No.	Mean Wt. (g)	95% C.L.
<i>carolinensis</i>			
First egg-3 days	98	9.75	0.21
4-12 days	230	9.88	0.14
13-21 days	53	9.76	0.28
<i>californicus</i>			
First egg-3 days	92	10.75	0.20
4-12 days	121	10.97	0.25
13-21 days	30	10.59	0.40
Both			
First egg-3 days	190	10.23	0.16
4-12 days	351	10.26	0.14
13-21 days	83	10.06	0.24

in our sample (1-3 per cent). Therefore, we do not believe this bias to be important in the oological data examined here. Furthermore, the data suggested that most egg collectors tended to collect eggs that were about one-third or less incubated (Table 1), thus eggs in late-stage incubation represented a small percentage of our sample. Although effects on the egg stemming from the age and physiology of the laying female would remain undetectable in oological samples, they would not be expected to affect an overall random, or essentially random, sample (see Asmundson et al., 1943).

Eggshell Changes and Pesticide Residues.—The small samples of post-1949 specimens suggested thinning in all eggshells measured (Table 4). Florida specimens showed a -17 per cent change in shell weight, Texas specimens a -20 per cent change, California specimens (Anacapa Is.) a -26 per cent change, and one set of eggs from Panama a -15 per cent change. All were significant ($P < 0.05$) changes. We could detect no change in shape in these post-1949 eggs ($P > 0.05$, Chi-square test). The incubation stages were essentially the same for both pre-1943 and post-1949 eggs (6 ± 2 days vs. 9 ± 5 days, 95 per cent C.L.). Size indices were not significantly different ($P > 0.05$), although the post-1949 eggs from Texas and Florida were slightly smaller in mean than those of pre-1943. Whether or not these changes in weight and thickness were associated with either recent declines of the Brown Pelican or environmental pollution, or both, remains to be determined.

Stickel (1968) has stated that in Gulf Coast Brown Pelicans, pesticide residues were of approximately the same general magnitude as those of herons

TABLE 4
POST-1949 EGG SHELL MEASUREMENTS OF BROWN PELICANS¹

Subspecies Area	<i>carolinensis</i> Florida	<i>carolinensis</i> Texas	<i>carolinensis</i> Panama	<i>californicus</i> California
Number	9	6	3	9
Wt. (g)	8.10	7.96	8.45	7.89
±95% C.L.	±0.14	±0.60	±0.99	±0.66
Size Index (cm ²)	36.5	37.6	37.6	39.0
±95% C.L.	±0.9	±2.4	±2.0	±1.4
No. Subelliptical	1	2	2	7
No. Oval	8	4	1	2
Thickness Index ²	2.22	2.12	2.25	2.02
±95% C.L.	±0.09	±0.10	±0.22	±0.12
Number	—	—	3	9
Thickness (mm)	—	—	0.457	0.424
±95% C.L.	—	—	±0.012	±0.018

¹ Post-'49 eggs were collected as follows: Florida—1950, 1953; Texas—1951; Panama—1952; California—1962.

² From Ratcliffe (1967): Thickness index = $10 \times \text{wt. in g} / (\text{length} \times \text{breadth in cm})$.

(*Ardea cinerea*) from Great Britain and Bald Eagles (*Haliaeetus leucocephalus*) in the United States (see Stickel et al., 1966; and Moore and Walker, 1964). Risebrough et al. (1967) analyzing two Brown Pelican eggs from the Gulf of California found them to be generally "low" in pesticide content (0.7 ppm [wet-weight basis] DDT and metabolites and about one-fifth as much polychlorinated biphenyls [PCB's], an industrial pollutant; endrin and dieldrin were also identified). They found an average of 0.8 ppm DDT-family residues (61 per cent DDE) and about two-thirds as much PCB in six Brown Pelican eggs taken in Panama. We converted the above residues to a ppm wet-weight basis by assuming 7 per cent fat in the eggs. We measured two of the eggshells from Risebrough's study (Baja California specimens) and found one suggestive of a "normal" egg (11.7 g, 0.59 mm in thickness) and the other suggestive of thinning (9.3 g, 0.50 mm). Another study (Anderson et al., 1969) showed that egg residues as low as 1 ppm of DDE, and possibly less, could be associated ($P < 0.05$) with detectable shell changes in White Pelicans, although egg residues may not always necessarily reflect residues in adults that could influence egg-shell deposition. Risebrough et al. (1967) reported 84.4 ppm of DDT-type residues, 91 per cent of which was *p,p'*-DDE (77 ppm) in the breast muscle of a Brown Pelican collected in California. These levels are only slightly lower than those reported from Lake Michigan Herring Gulls (*Larus argentatus*), which averaged 80 ppm DDE in the breast of adult birds (Hickey et al., 1966). Reproduction in the

TABLE 5
MEAN DATES OF CLUTCH COMPLETION IN BROWN PELICANS
FROM VARIOUS GEOGRAPHICAL AREAS

Area	No. Clutches	Mean Date \pm s.d.	Mean Stage Incubation ¹
So. California	29	8 April \pm 16 days	1.4
No. Baja California	61	10 April \pm 54 days	1.8
Texas	36	9 May \pm 18 days	1.5
Louisiana	14	27 April \pm 31 days	1.6
Florida	75	29 May \pm 125 days	1.9
South Carolina	14	5 June \pm 17 days	1.7

¹ Numerically coded with Table 1, cols. 1-2.

Wisconsin Herring Gull population in Green Bay (characterized by egg-breakage) is known to be severely affected by DDE and other residues (Keith, 1966; and Hickey and Anderson, 1968). Egg residues from the same population averaged 183 ppm DDE in 1963 and 1964 (Keith, 1966).

Breeding Characteristics.—Pacific Coast data suggested that between northern Baja California and California, the breeding dates were somewhat closely related (Table 5). Gulf and Atlantic Coast birds, on the other hand, showed much variation, especially in Florida (Appendix 1) as discussed by Bent (1922:295) and Palmer (1962:277). Palmer's (1962:275) distribution map suggests that on the Pacific Coast, the major breeding populations of *californicus* are concentrated into a smaller area than those from Gulf and Atlantic Coast sites (*carolinensis*). Bent (1922:296), Howell (1932:85-87), and Lowery (1960:113-114) noted that Brown Pelicans of the subspecies *carolinensis* tended to utilize trees as well as coastal beaches and islands as nesting substrates. Murphy (1936:810-814) mentioned diverse breeding sites for South American pelicans as well. The Brown Pelicans of northern Baja California and California seem more generally restricted to ground-nesting on islands (Bent 1922:301; Williams, 1927). Bond (1942) reported tree-nesting for the California Brown Pelican as very unusual.

In Florida, where the Brown Pelican still persists (Williams and Martin, 1969), a long breeding season and diversity of nesting substrate seem to characterize breeding. They nest year-round in Peru, although considerable shifting of sites occurs (Murphy, 1936:821-822). The Gulf of California Brown Pelicans still persist as breeders, although there is no evidence of a longer breeding season than in colonies farther north (R. W. Risebrough, pers. comm.).

Clutch sizes showed no significant variation ($P > 0.05$) between any of the geographical areas listed in Table 2. The means, and our best estimates for clutch-size in the Brown Pelican, are given in Table 1. Bent (1922:297),

and Palmer (1962:277) stated that three eggs, and less often two, is the normal clutch size; nests with four and five eggs have been found.

Breeding Records.—The population estimates by egg collectors cited in Appendix 1 must be viewed cautiously. These estimates were subject to observer error; however, they can provide an approximation of changes that might have occurred. Data-slip information, although most likely sketchy, can also provide documentation of past breeding locations. The records we found in egg collections did not provide a complete picture of breeding localities but suggested possible fluctuations in numbers over the years (Appendix 1). On the other hand, none of the major colonies seem to have been completely without birds since at least the late 1800's. Numbers probably increased on Anacapa Island, California, during the late 1920's. Williams (1927) reported a colony as far north as Point Lobos, California, during this time. The late 1920's may represent a period of population increase. Bond (1942) reported the estimated numbers on Anacapa Island from 1898 to 1941 to be highly fluctuating (estimates ran from about 200 to at least 2000 pairs). Banks (1966) reported eggs and young on Anacapa and essentially "normal" numbers of breeding birds, at least in 1963 and 1964, two years after the thin-shelled eggs reported here. The Los Coronados birds seem historically more stable (Appendix 1). It is certain that both Anacapa and Los Coronados breeders were historically present in large numbers (Banks, 1966). Risebrough (1968) and Schreiber and DeLong (1969) suggested that the Brown Pelican has decreased considerably in recent years off California, including no known breeders on Los Coronados in 1968. Perhaps the -20 to -26 per cent figure in shell change represents or approaches the lower limit to which eggs may survive to be collected by egg-collectors. Certainly, some production occurred in the California colony with these shell-changes, although present numbers suggest a declining population. Lowery (1960:113-114) mentions large colonies in Louisiana; yet Winckler (1968), in a popular article, summarized their nearly virtual disappearance from the Gulf Coast by 1968. In the light of the better-known demise of Gulf Coast Brown Pelicans, we believe the status of California Brown Pelicans and populations farther to the south needs immediate study.

SUMMARY

Mean clutch size in 236 sets of North American Brown Pelican eggs was 2.95 and did not vary geographically between North American populations. Shell weight varied from 8.05 g to 10.99 g along a geographic continuum. Shell thickness averaged 0.510 mm for *Pelecanus occidentalis occidentalis*, 0.554-0.557 mm for *P. o. carolinensis*, and 0.569-0.579 mm for *P. o. californicus*. The ranges of breeding dates for the more southern populations were wider than those of northern ones.

Small numbers of eggs taken in Texas and Florida after 1949 were 20 per cent below normal weight; 1962 eggs from California were 26 per cent below normal; and three

taken in Panama, 15 per cent below normal. Shell thickness had likewise decreased 15-27 per cent.

ACKNOWLEDGMENTS

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We are grateful to the many curators of museum collections listed in Appendix 1. The private collectors cited in Appendix 1 were extremely cooperative. We are especially grateful to Ed N. Harrison and Wilson C. Hanna for their personal assistance and extremely helpful suggestions. Mr. Harrison, in addition, located our 1962 samples of California eggs. Lucille F. Stickel and Eugene H. Dustman provided critical advice, and Ralph W. Schreiber suggested the immediate consolidation of our Brown Pelican data. Mrs. Pearl Davis punched our data cards, and the College of Agricultural and Life Sciences, University of Wisconsin, provided computer facilities at no cost. We are grateful to J. O. Keith and R. W. Risebrough for critical advice on the manuscript.

APPENDIX I

BROWN PELICAN BREEDING RECORDS TAKEN FROM NORTH AMERICAN
OOLOGICAL RECORDS AND COLLECTIONS.

Date	Location	Estimated Numbers; Remarks	Observer	Museum* of record
<i>Southern California</i>				
27 May 1893	Anacapa Is.	—	A. H. Miller	2
5 June 1910	Anacapa Is.	500+ pairs	G. Willett	3,5
7 Mar. 1916	Anacapa Is.	—	M. C. Badger	2
2 Mar. 1917	Anacapa Is.	—	M. C. Badger	3
15 May 1919	Anacapa Is.	—	—	1
7 Mar. 1920	Anacapa Is.	5,000+ pairs	S. B. Peyton	30
8 Mar. 1922	Anacapa Is.	—	S. B. Peyton	5
28 Mar. 1927	Anacapa Is.	—	—	3
24 Feb. 1929	Anacapa Is.	—	C. W. Ashworth	2
1 Mar. 1936	Anacapa Is.	—	E. Harrison	3
1 Mar. 1936	Anacapa Is.	2,000+ pairs	L. T. Stevens	14
12 Mar. 1939	Anacapa Is.	"large colony"	L. T. Stevens	4,7
19 May 1919	San Miguel Is.	—	—	1
25 May 1927	Point Lobos	8-10 nests	L. Williams (1927)	2
<i>Baja California, Mexico</i>				
18 Apr. 1894	Los Coronados	—	E. Parker	27
19 Apr. 1894	Los Coronados	—	—	1
4 Apr. 1895	Los Coronados	—	A. Hewitt	2,22
19 Apr. 1898	Los Coronados	—	A. J. Kellog	24
27 Apr. 1898	Los Coronados	—	—	3
6 May 1904	Los Coronados	—	O. C. Polling	2
6 Apr. 1908	Los Coronados	500 nests	P. I. Osborne	1,4

(APPENDIX I CONTINUED)

Date	Location	Estimated Numbers; Remarks	Observer	Museum* of record
6 Apr. 1908	Los Coronados	—	A. Van Rossem	25
1 July 1908	Los Coronados	—	P. I. Osborne	9
4 Apr. 1910	Los Coronados	—	P. I. Osborne	29
2 Apr. 1912	Los Coronados	—	C. S. Thompson	23
1 Apr. 1913	Los Coronados	500 nests	L. M. Huey	3
29 Mar. 1914	Los Coronados	—	W. C. Bradbury	2,9
31 May 1915	Los Coronados	—	I. D. Nokes	5
26 Mar. 1917	Los Coronados	500 pairs	N. K. Carpenter	6
4 May 1917	Los Coronados	—	D. S. DeGroot	2
11 Apr. 1919	Los Coronados	—	N. K. Carpenter	23
12 May 1921	Los Coronados	—	W. C. Hanna	4
30 Mar. 1922	Los Coronados	—	—	1
15 Apr. 1881	Mexican coast	—	—	1
26 Mar. 1917	So. Coronados, SE slope	—	—	1
6 Apr. 1920	Todos Santos Is.	—	G. Bancroft	4
6 Apr. 1920	Todos Santos Is.	—	J. Burnham	26
17 Apr. 1921	San Pedro Nolasco Is.	—	—	1
2 May 1921	Granite Is.	—	—	1
7 Apr. 1932	San Benito Is.	—	E. Harrison	3
10 Apr. 1932	San Martín Is.	—	E. Harrison	3
2 June 1932	Asunción Is.	—	E. Harrison	3
<i>Panama</i>				
15 Feb. 1942	Chama Is., Panama Bay, Panama	—	A. Wetmore	13
15 Mar. 1952	Taboga Is., Panama	—	A. Wetmore	13
<i>Texas</i>				
10 May 1886	Near Corpus Christi	—	F. B. Armstrong	12
20 May 1888	Neuces Co.	—	T. S. Gillin	4
10 Apr. 1889	So. Bird Is., Laguna Madre	—	J. A. Singley	2
16 Apr. 1889	So. Bird Is., Laguna Madre	—	J. A. Singley	4,25
14 June 1894	25 mi. from Corpus Christi	—	F. B. Armstrong	1
14 May 1896	So. Bird Is., Laguna Madre	—	D. B. Burrows	2
28 May 1910	Near Corpus Christi	—	C. E. Farley	30
30 May 1910	Near Corpus Christi	—	J. M. Carroll	4
3 May 1912	Laguna Madre	—	J. M. Priour	4
18 May 1913	Neuces Co.	—	F. B. Armstrong	9
27 May 1915	Padre Is.	—	F. B. Armstrong	2
19 May 1917	Big Bird Is., Laguna Madre	—	R. W. Quillan	19

(APPENDIX I CONTINUED)

Date	Location	Estimated Numbers; Remarks	Observer	Museum* of record
May 1919	Is. off so. coast	—	—	3
15 May 1919	Laguna Madre	—	H. Brandt	10
5 May 1922	Neuces Co.	—	G. Stewart	11
24 May 1925	Pelican Is., Aransas Bay	—	R. D. Camp	31
1951	Refugio Co.	—	T. C. Meitzen	18
<i>Louisiana</i>				
29 Mar. 1893	Lost Is.	—	F. A. McIlhenny	2
28 Mar. 1894	Marsh Is.	—	F. A. McIlhenny	2
29 Mar. 1894	Shell Keys	—	F. A. McIlhenny	2,23
3 June 1919	Pass à l'Outre	—	E. R. Kalmbach	13
5 June 1919	Errol Is.	—	J. D. Figgins	9
26 May 1938	North Is.	—	F. Tobin	10
13 Apr. 1940	La Fourche Par., Timbalier	—	G. H. Lowery (1960)	17
<i>Florida</i>				
15 Mar. 1879	Near Marco	—	—	1
1 Apr. 1880	Indian R.	—	C. L. Cass	26
15 Apr. 1880	Indian R.	—	—	1
29 Apr. 1880	Old Tampa Bay	—	—	1
12 Apr. 1890	Lee Co.	—	H. R. Jamison	4
12 Apr. 1890	Charlotte Harbor	—	S. Reiff	21
3 May 1890	W. of Pine Is., Lee Co	225 nests	N. K. Jamison	4
26 Apr. 1891	Pelican Is.	—	M. Gibbs (1894)	9
12 Apr. 1892	Tampa Bay	—	D. P. Ingraham	27
10 May 1893	Pelican Is.	—	J. M. Southwick	4
5 June 1893	Mullett Key	—	B. T. Smith	26
30 June 1894	Tampa Bay	—	—	1
21 Jan. 1896	Pelican Is.	500 pairs	B. W. Evermann	23
3 Apr. 1896	Pelican Is.	—	H. E. Pendry	3
30 Apr. 1896	Seminole Is.	—	H. E. Pendry	5
18 May 1896	Rookery Is., off Diston City	—	W. Mcyor	8
15 May 1899	Brevard Co.	—	F. S. Webster	10
19 Apr. 1908	Boca Grande, Charlotte Keys	200 birds	P. B. Phillipp	12
20 Apr. 1908	Charlotte Harbor, Devilfish Key	—	P. B. Phillipp	12
3 May 1911	Pelican Is.	—	P. B. Phillipp	12
19 May 1911	Hillsborough Co.	—	O. E. Baynard	24
27 Apr. 1913	Lec Co.	—	O. E. Baynard	3,9
27 Apr. 1913	Roco Bay, Pinellas Co.	large colony in trees	O. E. Baynard	8

(APPENDIX I CONTINUED)

Date	Location	Estimated Numbers; Remarks	Observer	Museum* of record
15 May 1918	Tampa Bay	—	J. L. Vaughn	4
20 Apr. 1920	Tampa Bay	—	—	3
17 May 1921	Tampa Bay	—	J. L. Vaughn	2,20
17 May 1921	Tampa Bay	—	W. F. Lewis	8
27 May 1921	Tampa Bay	—	J. L. Vaughn	23
28 Dec. 1921	Pelican Is.	—	T. D. Burleigh	10
20 Apr. 1926	Pinellas Co.	—	C. E. Doe	16
1 June 1926	Merritt Is.	—	K. Squires	2
10 June 1929	Merritt Is.	2,500 pairs	J. C. Howell, Jr.	12
28 Mar. 1930	Lee Co.	—	C. E. Doe	16
25 Apr. 1930	Near Bokelia?	—	C. E. Doe	16
10 Apr. 1931	Mosquito Lagoon, Brevard Co.	2,000± nests	W. H. Nicholson	23
6 June 1931	Pine Is. Res., Bird Key	—	R. W. Williams	13
7 June 1931	Matlacha Pass Res., 6-mi. Is.	—	R. W. Williams	13
3 May 1932	Bird Key, Hillsborough Co.	—	R. E. Gammell	7
22 Apr. 1934	Rattlesnake Key, Levy Co.	—	C. E. Doe	16
9 Mar. 1950	Is., n. side of Cocoa— Cocoa Beach	375 nests	C. E. Carter	15
10 Mar. 1953	Merritt Is.	—	H. Brandt	10
<i>Georgia</i>				
16 June 1898	Chatham Co.	on beach	T. D. Perry	1,16
<i>South Carolina</i>				
10 May 1901	Bird Bank, Bull's Bay	—	M. T. Cleckley	9
20 June 1901	Near Charleston	on beach	—	3
23 June 1901	Bay Point, near Beaufort	"large colony"	M. T. Cleckley	3
23 May 1915	Bird Bank, Bull's Bay	—	A. C. Bent	13
18 June 1915	Bird Bank, Bull's Bay	—	A. Sprunt, Jr.	30
7 July 1916	Bull's Bay	—	M. T. Cleckley	28
3 June 1925	Bull's Bay	—	W. B. Savary	5
14 June 1934	Georgetown Co.	—	H. L. Harllee	14
20 June 1942	Bull's Bay	—	E. J. DeCamps	14
10 June 1943	St. Helens Sound, Beaufort (Bird Bank)	—	E. J. DeCamps	4
10 July 1943	18 mi. e. Beaufort	—	E. J. DeCamps	14
<i>Cuba</i>				
8 Sep. 1930	Cacachita Bay	—	P. Bartsch	13

* Museums and collections are numbered as follows: 1. Calif. Acad. Sci., San Francisco; 2. Mus. Vert. Zool., Univ. Calif., Berkeley; 3. Western Found. Vert. Zool., Los Angeles, Calif.; 4. San Bernardino Co. Mus., San Bernardino, Calif.; 5. S. B. Peyton, private collection, Fillmore, Calif.; 6. Oakland Publ. Mus., Oakland, Calif.; 7. Santa Barbara Mus. Nat. Hist., Santa Barbara,

Calif.; 8. San Diego Mus. Nat. Hist., San Diego, Calif.; 9. Denver Mus. Nat. Hist., Denver, Colo.; 10. Carnegie Mus., Pittsburgh, Pa.; 11. Philadelphia Acad. Sci., Philadelphia, Pa.; 12. Amer. Mus. Nat. Hist., New York, N.Y.; 13. U.S. Natl. Mus., Wash., D.C.; 14. Zoological Mus., Clemson Univ., Clemson, S.C.; 15. C. E. Carter, private collection, Orlando, Fla.; 16. Fla. State Mus., Gainesville; 17. L.S.U. Mus. Nat. Sci., Baton Rouge, La.; 18. T. C. Meitzen, private collection, Refugio, Tex.; 19. R. W. Quillan, private collection, San Antonio, Tex.; 20. Univ. Kans. Mus. Nat. Hist., Lawrence; 21. Univ. Nebr. Zool. Dept. Mus., Lincoln; 22. Cleveland Nat. Sci. Mus., Cleveland, Ohio; 23. Royal Ont. Mus., Toronto; 24. Joseph Moore Mus., Earlham Coll., Richmond, Ind.; 25. Ohio State Mus., Ohio State Univ., Columbus; 26. Univ. Mich. Mus. Zool., Ann Arbor; 27. James Ford Bell Mus. Nat. Hist., Univ. Minn., Mpls.; 28. M. Pollock, private collection, Edmonton, Alta.; 29. Burke Memorial Mus., Univ. Wash., Seattle; 30. Puget Sound Mus. Nat. Hist., Univ. Puget Sound, Tacoma; 31. Zoology Mus., Ore. State Univ., Corvallis.

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NICHE OVERLAP IN FEEDING ASSEMBLAGES OF NEW GUINEA BIRDS

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A SINGULAR opportunity for assessing the degree of niche overlap among elements of tropical avifaunas exists in the phenomenon of feeding trees. These contain fruit, flowers or some other food source that attracts numbers of animals, among which birds usually predominate. Since only a single commodity is available in most feeding trees, it is possible to compare the harvest by different species through some appropriate measure of tree usage. Consumption of a common resource by a number of species implies niche overlap and suggests that a state of competition at least potentially exists among the species.

The striking concentrations of birds that are frequently attracted to feeding trees in New Guinea have been remarked upon previously by observers working at widely scattered localities (Mayr and Rand, 1937; Rand, 1942*a* and *b*; Ripley, 1964). In their recent Handbook of New Guinea Birds, Rand and Gilliard (1967) comment on the significance of this phenomenon and point out the need for a systematic study.

The present paper gives an account of observations made at 20 feeding trees in the Eastern Highlands District of the Territory of New Guinea. Repeated censuses of the bird assemblages in each tree led to a time-dependent measure of feeding for each species present. The results allow estimates of the degree of niche overlap among the species taking certain classes of food (e.g., flowers, small fleshy fruits) and indicate the diversity of food sources exploited by particular species or groups of species.

METHOD

On finding an active feeding tree the observer sought the most advantageous viewing station, i.e., the point on the ground from which optimal lighting and visibility of the crown was obtained. In exceptional cases the entire face of a tree could be observed, but far more commonly intervening foliage reduced the exposure to a part of the crown or even a few branches. Consequently a large fraction of the birds using most trees was not seen.

Each tree studied was observed for one to several $\frac{1}{2}$ or 1 hour periods, each of which was comprised of a succession of two-minute censuses. The exposed portion of the feeding tree was systematically scanned with a pair of 8 \times 30 binoculars for approximately 1 minute and 45 seconds. During this time the observer accrued a mental tally of all the species and individuals seen. The remaining 15 seconds of these censuses were used to record the data. The two-minute census was selected when it was found that this was about the maximum time over which the observer could keep track of a cumulative mental tally of species and individuals in an active tree. It was a policy to maximize

the number of individuals rather than distribute the observation time evenly over all parts of the tree. No particular effort was made to find different birds with each new census, and thus the same individuals were often reeorded for a number of successive censuses.

A unit of tree-usage was derived from the census data on the assumption that a single sighting represented an average stay of two minutes in the tree. The justification of this assumption lies in the fact that the canopy area under observation was generally several times larger than that covered in one binocular field. Thus it was possible, on the one hand, for birds to come and go from the visible portion of the tree and escape detection, and on the other, for birds to remain visible for nearly 4 minutes and yet be reeorded in only one census. Since each observation represents a bird-usage of 2 minutes, the identification of one bird in each of the 30 censuses in a one-hour observation period would add up to a total of one bird-hour of tree usage. The number of bird-hours recorded in an observation period of any length is thus the aggregate of individual sightings divided by the number of two-minute censuses.

Once it had been ascertained several times that a species was actually taking food, all further individuals were tallied on the premise that they were in the tree for the purpose of feeding. The unexpected scarcity of transient species in feeding trees made it evident that virtually all the birds recorded in them had entered specifically to feed. In general the majority of individuals in a tree at any time were actively feeding, though social interactions or periods of rest or preening resulted in frequent brief interruptions.

The identification of more than 90 per cent of the bird species included in this report was confirmed by specimens collected in the localities of the trees but not from the trees themselves. Nomenclature follows that of Rand and Gilliard (1967). The feeding trees unfortunately cannot be identified since our collection of preserved plant material was lost. Thus brief descriptions from our field notes of the trees and their flowers or fruits must suffice.

All of the observations were made during the period of June to August, 1964, in the Eastern Highlands District of the Territory of Papua and New Guinea. A synopsis of the localities mentioned in the text follows. Karimui Patrol Post lies about 70 miles southwest of Goroka at 3,650 feet in an extensive mountain basin. Udo, Mao, Sordida, and Palea are native hamlets in the vicinity of Karimui. A flowering tree on the north bank of the Sena River was about 14 miles northeast of Karimui at an elevation of approximately 4,500 feet. A fruit tree near the village of Mengino I was at about 4,800 feet on the west slopes of Mt. Michael in the area administered from Lufa Patrol Post. Two localities were villages in the Fore language are administered from the Okapa Patrol Post, which is 36 miles southeast of Goroka: Miarassa at 5,800 feet and Okassa at about 3,500 feet.

RESULTS

Bird-usage data were recorded from nine flowering trees or lianas of four species, ten fruiting trees of at least six species, and one tree whose bark attracted large numbers of parrots. We will consider results from each of these general classes of feeding trees in order.

FEEDING ASSEMBLAGES IN FLOWERING TREES

White-flowered trees.—We were fortunate in locating five individuals of one species of flowering tree within a radius of 1½ miles of Karimui Patrol Post. These trees carried great numbers of dense umbel-like flower heads.

The individual blossoms were 3–4 mm across with conspicuous white petals and somewhat swollen glandular receptacles. All but one of the five trees stood at the edge of wide trails through original forest, the exception (Udo-2) being located in the forest some 200 yards to the side of a trail. Estimates of their heights fell between 100 and 120 feet, of which their leafy crowns comprised the upper 30–50 feet.

The bird usage of these trees was recorded in 2 to 5 one-hour observation periods. The results of repeated observations at a single tree showed little variation in the rank order of the 6 most frequent species (Table 1A). Bird-hour totals varied somewhat more and were particularly influenced by the large groups of lorikeets whose movements in and out of the tree were erratic. In general, the variation in results from different trees of the same species was greater than that among different readings from the same tree.

Averaged records from the five white-flowered trees are given in Table 1B. The preponderance of honeyeaters is immediately apparent. Members of this family alone accounted for 67–88 per cent of the species seen in these trees but comprised only 53 per cent of the observations. The small lorikeet, *Charmosyna placentis* was by far the most numerous species and accounted for 37 per cent of all observations. The list of species showed little variation from one tree to another, most of the exceptions being transients or occasional visitors. Of the 11 species that were regular users of these trees, all 11 occurred at two trees, 10 at one tree, and 9 at the remaining two trees.

While these trees were under observation, it became apparent that two of them were giving anomalous results with respect to the frequencies of some species. The third Udo tree attracted extraordinary numbers of *Oedistoma pygmaeum* and the *Myzomela* honeyeaters, while *Oreornis obscurus* was comparatively scarce. In contrast, at the Sordida tree the frequency of *Myzomela nigrita* was a factor of 10 less than in the third Udo tree and that of *Oreornis obscurus* was 30 times greater while *Myzomela cruentata* was altogether absent.

We suspected that these anomalous frequencies may have resulted from the facts that only the topmost branches of the third Udo tree were visible and that only the lower portion of the crown of the Sordida tree could be observed. This possibility was tested with the three white-flowered trees whose full crowns were visible. All subsequent observations on these trees noted whether the birds had been seen above or below imaginary horizontal bisectors of the crowns. A total of 965 sightings of 10 species were distributed, 51 per cent in the upper and 49 per cent in the lower halves of the crowns (Table 2). All but *Charmosyna placentis*, *Toxorhamphus iliolophus*, and *Xanthotis polygramma* were more or less unevenly distributed. The species that were disproportionately abundant in the third Udo tree, *Oedistoma pygmaeum* and the three *Myzomela* honeyeaters, were found to keep largely

TABLE 2

VERTICAL DISTRIBUTION OF SOME BIRD SPECIES IN THREE WHITE-FLOWERED TREES
IN THE KARIMUT REGION. PROBABILITIES FROM TWO-TAILED STANDARD
NORMAL VARIABLE TEST.

Species	No. of Observations	Per cent in Upper Half	Per cent in Lower Half	P
Parrots				
<i>Chamosyna placentis</i>	214	48	52	0.32
Honeyeaters				
<i>Oedistoma pygmaeum</i>	176	66	34	0.001
<i>Myzomela eques</i>	9	67	33	0.33
<i>Myzomela cruentata</i>	2	100	0	—
<i>Myzomela nigrita</i>	77	94	6	0.001
<i>Toxorhamphus iliolophus</i>	25	52	48	0.92
<i>Oreornis obscurus</i>	14	0	100	0.001
<i>Xanthotis chrysotis</i>	101	31	69	0.001
<i>Xanthotis polygramma</i>	79	46	54	0.35
<i>Meliphaga</i> spp. (six species)	256	36	64	0.001
Total	965	51	49	

to the upper branches. On the other hand, *Oreornis obscurus* appeared exclusively in the lower branches of the test trees, thus accounting for its extreme scarcity in the third Udo tree and relative abundance in the Sordida tree.

These data suggest that much of the observed tree-to-tree variation was due to fortuitous differences in the visibility of the canopy. When these differences are taken into consideration it is apparent that the pattern of usage of the 5 white-flowered trees was notably consistent. As the minimum distance between any two of these trees was approximately $\frac{1}{4}$ mile, there was probably very little overlap in the populations of most passerine species that were using them. Back and forth movements of lorikeets were much more likely, since they always travelled in flocks which appeared to range over wide areas. Consequently, usage data were least consistent for lorikeets, which at any moment were either present in numbers or altogether missing.

Lavender-flowered climbers.—The question of how as many as a dozen species of nectar-feeding birds can share a common food source may in part be answered by the degree of ecological isolation afforded by vertical stratification. The effectiveness of this behavioral mechanism in achieving a partial separation of potential competitors is indicated by the results from two flowering climbers. These enveloped the trunks of forest trees located at the edge of trails where more sunlight entered than in the heart of the forest.

Somewhat drooping horizontal branches carried at their ends large showy panicles of lavender campanulate flowers 4–6 mm across. The foliage and flowers were borne from about 15 feet above the ground to the base of the canopy at about 75 feet.

The combined results of 7 one-hour observation periods at two of these climbers located about 2 miles apart are given in Table 4. Of the 11 species of lorikeets and honeyeaters that were regular users of the white-flowered trees, seven were also frequent at the climbers. The four missing species were honeyeaters, *Toxorhamphus iliolophus* and the three *Myzomela* species, of which the *Myzomelas* had all shown strong affinities for the upper layer of the canopy. *Oedistoma pygmaeum*, which was also found to inhabit the upper canopy, was approximately 30 times less frequent in the climbers than in the white-flowered trees. The two honeyeaters that appeared in the climbers but not in the white-flowered trees, *Glycichaera fallax* and *Pycnopygius ixoides*, not unsurprisingly, are birds of the understory. *Glycichaera* is apparently a rarity at Karimui, since we were unable to obtain a specimen and have no other records of it.

On the basis of measured and observed vertical distributions of flower feeding birds at Karimui, we have compiled a list of species ranked in order of their presumed elevational preferences from the top of the canopy downwards (Table 3). By far the largest group (II) is composed of species that range more or less freely through a large part of the vegetational column. The *Myzomela* honeyeaters of group I appear to live exclusively in the high canopy from 80–150 feet above the forest floor. The birds of group III range up to 30–50 feet but rarely if ever use exposed crowns for feeding. Niche overlap between the species of groups I and III is thus almost entirely avoided. Maximum niche overlap occurs between the species within a group. Varying degrees of interaction can be expected between the birds of group II and those of groups I and III.

Overall usage of the flowering climbers, as with the white-flowered trees, was heavily dominated by lorikeets and honeyeaters (91 per cent). *Macropygia* sp. (6 per cent) and *Zosterops minor* (2 per cent) made up most of the remainder, the latter also having occurred less frequently in the white-flowered trees. The seven species that were regular in both the white-flowered trees and the climbers (*Trichoglossus haematodus*, *Charmosyna placentis*, *Oedistoma pygmaeum*, *Oreornis obscurus*, *Xanthotis chrysotis*, *X. polygramma*, and *Meliphaga* spp.) comprised 82 per cent of the total usage of the former and 83 per cent of the latter. This result implies particularly broad niche overlap between these species despite considerable differences between many of them in size and structure.

Hibiscus flowers.—A third type of flowering tree at Karimui deserves

TABLE 3

LIST OF BIRD SPECIES FEEDING ON FLOWERS IN THE KARIMUI REGION IN ORDER OF PRESUMED ELEVATIONAL PREFERENCE IN FOREST VEGETATION.

Variety of feeding trees used by each species is indicated in the right hand column.

F = flowers; SF = small fruits; *Ficus* = *Ficus* fruits; B = bark excrecence.

Group	Species	Elevational Preference	Classes of feeding Trees Visited
I	<i>Myzomela cruentata</i>	upper canopy only	F
	<i>Myzomela nigrita</i>		F
	<i>Myzomela eques</i>		F
II	<i>Oedistoma pygmaeum</i>	canopy and middle levels	F
	<i>Toxorhamphus iliolophus</i>		F
	<i>Charmosyna placentis</i>		F,B
	<i>Xanthotis polygramma</i>		F,SF, <i>Ficus</i>
	<i>Meliphaga</i> spp.		F,SF, <i>Ficus</i>
	<i>Xanthotis chrysotis</i>		F,SF, <i>Ficus</i>
	<i>Trichoglossus haematodus</i>		F, <i>Ficus</i> ,B
	<i>Oreornis obscurus</i>		F,SF, <i>Ficus</i>
III	<i>Zosterops minor</i>	middle and lower levels exclusive of canopy	F
	<i>Macropygia</i> sp.		F,SF
	<i>Pycnopygius ixoides</i>		F,SF

mention because of its location at the edge of a native garden perhaps a half-mile from the nearest forest. A small spreading tree of the *Hibiscus* tribe, it carried numbers of showy red blossoms 4 to 6 cm across. In one hour we recorded 2.4 bird-hours of usage, all by small bands of the sylviid, *Gerygone chloronota* (Table 4). These birds always moved together in groups of 2-6 and kept up a nearly continuous flow of soft vocalizations while they probed between petals at the bases of the large corollas. Although we visited this tree on several occasions, none of the forest nectar feeders was observed there. This negative result may not be significant in itself, but reinforces our general impression that open and second growth habitats in New Guinea have notably impoverished avifaunas in comparison, for example, with tropical South America (Diamond and Terborgh, 1967). The virtual absence of such habitats above 1,000 feet over most of the island prior to the recent expansion of the native population in the highlands is probably the explanation for this fact.

River Sena orange-flowered tree.—Observations at a fourth type of flowering tree were made at a locality lying a full day's walk to the northeast of Karimui at an elevation approximately 850 feet higher (about 4,500 feet). This tree overhung the north bank of the Sena River and was viewed con-

veniently from a large boulder in midstream. Its relatively small crown overtopped the nearby foliage and rose well over 100 feet above the forest floor. A heavy bloom of tiny flowers, 3–5 mm in diameter borne in dense heads, gave a yellow-orange cast to the whole crown. *Oedistoma* and *Myzomela* honeyeaters accounted for an unusually high portion of the usage (67 per cent), a finding that corroborates the observation that these species concentrate their feeding in the highest parts of the canopy. The species composition of the feeding assemblage was not one that would have occurred at Karimui. The presence of *Charmosyna pulchella*, *Myzomela cruentatus*, *M. rosenbergii*, and *Melidectes torquatus*, all absent or uncommon at Karimui, can best be attributed to the higher elevation of the Sena River site, since these are known to be montane rather than lowland forms (Mayr, 1941). The absence of some expected species (e.g., *Meliphaga* sp.) was perhaps due in part to the height and consequent exposure of this tree and to the fact that only one hour of observation was possible. Nevertheless, the total usage by families was in accord with the pattern that prevailed at Karimui, namely a predominance of honeyeaters (79 per cent), followed by lorikeets (20 per cent) and a very small remainder (1 per cent).

FEEDING ASSEMBLAGES IN FRUITING TREES

Most of the fruiting trees in which we found feeding birds could readily be placed in one of two categories: Those that bore small (< 5 mm) fleshy fruits and attracted a large variety of bird species, and those which bore larger (> 10 mm) fleshy fruits that were evidently unmanageable for small birds.

Small fruits.—We shall first consider trees with small fleshy fruits, in particular a set of three large strangling figs. These appeared, on examination of their fruits and foliage, to be of the same species, though possibly they were closely related species. All were of great stature (at least 100 feet), had broadly spreading crowns, and were heavily laden with soft pinkish fruits 4–6 mm in diameter. At Sordida (3,650 feet) one of these stood alone in an area that had been recently cleared for native gardens. The clearing was surrounded on all sides by forest which came to within 35 yards of the strangler. Another of these trees was located in dense forest at 3,500 feet in the bottom of a ravine about 14 miles southeast of Okapa Patrol Post. The third fruiting strangler was in montane forest at 5,800 feet near the Fore village of Miarassa.

The results of five, three and four observation periods at these three trees, respectively, are given in Table 4. The number of species that regularly fed in the stranglers was only slightly greater on the average than in the Karimui white-flowered trees, but included a notably greater variety of

families. Whereas each of the white-flowered trees at Karimui attracted eight to ten species of honeyeaters, none of the stranglers was used by more than three species of any family. Pigeons and honeyeaters were numerically dominant and accounted for 52–79 per cent of the total usage. Members of ten other families comprised the substantial remainder, again in contrast with the flowering trees in which the two principal families, honeyeaters and parrots, accounted for 91–99 per cent of the usage.

In consequence of the marked altitudinal turnover of bird faunas in New Guinea, the bird assemblages found in the three stranglers had very few species in common. The Sordida and Okassa trees shared only four out of a total of 25; the Sordida and Miarassa trees may have had one common species of *Meliphaga* out of 24, and the Okassa and Miarassa assemblages shared five out of 19. Members of four families occurred in all three of the stranglers and members of five more used two of them. In view of the great differences in habitat at each of the sites, such consistency implies that the pattern of usage of a given food source is to some measure independent of elevation and the particular species involved.

Some of the obvious differences in the data from the three stranglers can probably be ascribed to site-specific factors. The relative scarcity of honeyeaters in the Sordida tree and the abundance of *Mino dumontii*, a bird of second growth and edges, are surely due to its exposed position in a native garden. Low numbers of both species and individuals were recorded for the Miarassa tree, not as a result of low usage, but of exceptionally poor visibility of the crown from the only suitable viewing station.

Two additional species of trees with small (3–5 mm) fruits were the subjects of less intensive observations (Table 4). One was located in tall forest near Udo in the Karimui region and the other in old second growth near the Gimi Village of Mengino I on the west slope of Mt. Michael. The bird assemblages in these trees differed from those in the stranglers in attracting smaller numbers of species and families and in the preponderance of honeyeater usage. Since the results are based on only one and three hours of observation, respectively, the species lists are unrealistically low. Nevertheless, the scarcity (absence) of parrots, and the presence of pigeons, cuckoo-shrikes, whistlers, and flowerpeckers, is similar to the pattern found in the stranglers and quite unlike that of any of the flowering trees.

Large fruits.—Larger fruits were consumed almost exclusively by pigeons. Typical results are given in Table 4. The two trees held heavy crops of soft olive-sized fruits and in both the feeding was confined to two species of pigeons. In contrast with the sustained use of trees bearing flowers or small fruits, the presence of birds at sources of large fruits was sporadic and unpredictable. The trees were generally vacant for most of the day and when

a group of pigeons did arrive, it seldom remained for as long as an hour. Most of the flocks of feeding pigeons that came to the observer's attention contained a single species only. The large parrots and hornbills that might be expected to feed on large fruits in company with pigeons were never seen to do so. The population densities of these birds in the localities we visited were, however, low, and the large parrots are generally shy.

Ficus fruits.—An intriguing exception to the usual absence of passerine birds from trees with large fruits was uncovered in the case of three trees of a *Ficus* species (Table 4). Two were in tall forest along the Udo road near Karimui, while the third was in a grove of *Casuarina* second growth at an elevation of 5,800 feet near Mirassa. The fruits were ovoid-cylindrical, 6–8 cm in length and 3–4 cm in diameter. A thick woody pericarp precluded any direct assault on the sweet seedy pulp within. Nevertheless, examination of fallen fruits indicated that most had been entered by neatly cut holes, about 1 cm in diameter, in the blossom ends. Observation of the feeding birds soon disclosed that the holes were made by lorikeets. Tossing chips aside with a shake of the head, they gained access to the pulp within 5 minutes. Apparently, the side walls of the pericarp were invulnerable even to the lorikeets, because they always abandoned the fruits with most of the pulp remaining. The preopened fruits then attracted many other species, principally honeyeaters whose long and delicate bills are well-suited for probing but quite incapable of opening these fruits.

The second Udo *Ficus* (Table 4) was observed at an early stage in ripening when it held an abundance of unopened fruits which attracted lorikeets (> 99 per cent of usage), but before it contained sufficient numbers of opened fruits to be of interest to other birds. The first Udo tree and the Mirassa tree were at a later stage by which parrot usage had declined to only 8 per cent and 6 per cent, respectively, of the total. Honeyeater usage, on the other hand, had mounted to 90 per cent and 93 per cent.

A clear example of the dependence of feeding capabilities on bill structure, this extraordinary situation produced a pattern of tree usage reminiscent of both flowering and fruiting trees. The absence of pigeons and 95–100 per cent usage by parrots and honeyeaters are suggestive of the former, while the presence of cuckoo-shrikes, whistlers, and flowerpeckers is typical of the latter.

Bark feeding.—While at Karimui we encountered an active feeding tree whose attraction was apparently either a sap exudate or excrescences on the bark produced by an infestation. The several bands of parrots that were using this tree restricted their attentions to the smooth pale gray bark of the upper trunk and main branches (Table 4). All four species appeared to use the same method of feeding which consisted of slowly working up or down

TABLE 4 (Continued)

Hours of Observation	Flowers			Small Fruits			Large Fruits		Ficus Fruits		Bark Feeding			
	White-flowered trees	Lavender-flowered vines	River Sena flowering tree	Hibiscus flowers	Sordida strangler	Okassa strangler	Miarassa strangler	Mengno fruiting vine	Udo fruit tree	Okassa fruit tree		Sordida fruit tree	First Udo <i>Ficus</i>	Second Udo <i>Ficus</i>
<i>Cicinnurus regius</i>	18	7	1	1	5	3	4	3	1	1	1	3	1	3
<i>Paradisaea apoda rudolphi</i>	<1	<1	1	2	1									<1
Honeyeaters	53	79	78	4	4	66	10	88	88	88	88	90	1	93
<i>Glycichaera fallax</i>	8	3	32											
<i>Oedistoma pygmaeum</i>	3	<1												
<i>Myzomela eques cruentata</i>	1		17											
<i>nigrita</i>	10		1											
<i>rosenbergii</i>	<1		17											(t)
<i>Toxorhamphus iliolophus</i>	2													
<i>Melilestes megarhynchus</i>							3							<1
<i>Melipotés jumigatus</i>	<1		2											92
<i>Melidectes torquatus</i>	3	5												
<i>Oreornis obscurus</i>	8	19		3	37			7	10	(t)		3	1	
<i>Xanthotis chrysolis polygramma</i>	6	11						2	2			24	17	

TABLE 4 (Continued)

Hoursof Observation	Flowers		Small Fruits				Large Fruits		Ficus Fruits		Bark Feeding				
	White-Flowered trees	Lavender-Flowered vines	River Sena flowering tree	Hibiscus flowers	Sordida strangler	Okassa strangler	Miarassa strangler	Mengino fruiting vine	Udo fruit tree	Okassa fruit tree		Sordida fruit tree	First Udo Ficus	Second Udo Ficus	Miarassa Ficus
<i>Meliphaga</i> spp. (\leq six species)	12	37	1	1	10	3	3	76	66	1	1	46	1	1	1
<i>Pycnopygius cinereus</i> <i>ixoides</i>	<1	4	10		19	3	3	1	7						(t)
Unidentified honeyeaters															
Flowerpeckers															
<i>Dicaeum geelvinkianum</i>			1		4	14	3	3							<1
<i>Melanocharis longicauda</i> <i>versteri</i> <i>striativentris</i>			1		4	4	2	2							<1
White-eyes	<1	2													
<i>Zosterops minor</i>	<1	2													
Unidentified	1														
Total No. Species	17	16	7	1	15	14	10	9	9	2	2	7	2	7	4
Mean Total Bird-Hours	5.68	3.77	2.93	2.37	5.89	2.67	0.63	1.33	1.96	3.63	1.47	2.87	8.00	12.37	7.63

open sections of bark while chewing actively with the sides of their beaks pressed to the surface. Their efforts appeared to be concentrated around cracks, knotholes, and scars. The crown of the tree was nearly 100 feet above the viewing station and could not be seen in sufficient detail to permit identification of the food material.

The appearance of *Loriculus aurantiifrons* in this tree represents our only record of the species in the Karimui region. The other 3 parrots were common in the area and frequent visitors at feeding trees. *Charmosyna placentis* was the most abundant user of flowering trees but was not seen taking fruit. *Trichoglossus haematodus* regularly frequented both fruiting and flowering trees while *Psittaculirostris desmarestii* occurred commonly in fruit trees but was seldom attracted to flowers. Only in the present instance did we find all three species together in numbers that corresponded with our impression of their relative abundances in the local fauna.

NICHE OVERLAP IN FEEDING TREES

The number of bird species that use a feeding tree depends largely on the class of food available rather than on the particular species of tree (Table 4). Large fruits, bark excrescences, *Ficus* fruits, flowers, and small fruits, in that order, attract feeding assemblages of increasing diversity. High species totals for two of the flowering trees are the result of lumping data from more than one tree, whereas this was not done for any of the fruit trees. The fact that large fruits attract the least number of bird species and small fruits the most clearly illustrates the limitation that body size imposes on the size range of food taken. The high diversity of the assemblages that feed on small fruits results partly from the fact that the fauna contains a preponderance of small species and partly because the larger species often take small foods whereas the converse is not possible.

In trees bearing flowers, small fruits, or mature *Ficus* fruits we found only four instances in which more than 50 per cent of the bird usage was confined to the members of a single genus. The comparatively low niche overlap in three of these (Mengino fruiting liana, the *Hibiscus* and the *Miarassa Ficus*) was probably due to the location of the trees in second growth where the number of bird species is drastically lower than in the forest. The remaining case was the Udo fruit tree in which 66 per cent of the usage was by one to several species of *Meliphaga*. It is apparently rare that forest feeding trees are dominated to such an extent by one genus. Field identification of particular species of *Meliphaga* is at best difficult but at Karimui is rendered impossible by the presence of six species, five of which are scarcely distinguishable in the hand.

A quantitative estimate of the niche overlap in feeding trees can be obtained

TABLE 5

NICHE OVERLAP IN FEEDING TREES FROM THE POINT OF VIEW OF THE AVERAGE USERS.
The average user of a tree is the species whose usage brings the cumulative total to 50 per cent or more in a ranking of the species by usage.

Food Source	Average User	Per cent of Total Usage By Average User	Per cent of Total Usage By Species In Other Genera	Per cent of Total Usage By Species In Other Families
Flowers				
Karimui white-flowered trees (5)	<i>Myzomela nigrita</i>	10	86	47
Karimui lavender-flowered vines (2)	<i>Xanthotis chrysotis</i>	19	71	24
Sena River orange-flowered vines (2)	<i>Charmosyna pulchella</i> and <i>placentis</i>	<20	80	80
Small Fruits				
Sordida strangler	<i>Psittaculirostris desmarestii</i>	30	70	70
Okassa strangler	<i>Pycnopygius cinereus</i>	19	81	34
Miarassa strangler	<i>Pitohni dichrous</i>	10	90	85
Mengino fruiting vine	<i>Meliphaga</i> ssp.	?	24	12
Udo fruit tree	<i>Meliphaga</i> spp.	?	34	12
Mean			67	46

by computing the proportion of the total usage that accrues to the average user (Table 5). The average user is here defined as the species whose usage brings the cumulative total to 50 per cent or more in a ranking of the species by usage. In those cases in which the average user was identified to species it accounted for no more than 30 per cent of the total usage. Conversely, a mean of 67 per cent of the usage was by species in other genera and 46 per cent by species in other families in all the trees that contained either flowers or small fruits. It must be remembered that these figures are low estimates because of the probable but unrecorded utilization of these food sources by mammals, insects and even microorganisms.

DISCUSSION

In commenting on some feeding assemblages in Colombia Willis, (1966) concluded that because the food supply in most feeding trees appears to be superabundant, the competition between the species using them is probably insignificant. This inference tacitly depends on the regular availability of

feeding trees, an eventuality not borne out by our experience. We have on numerous occasions walked as much as an entire day in quest of feeding trees, both in New Guinea and in South America, without encountering a single one. The climate in the Eastern Highlands of New Guinea undergoes only a limited and irregular variation, yet it was our impression that flowering and fruiting of trees is highly sporadic. Similar impressions have been gained by botanists travelling in many parts of the tropics (Richards, 1952). Moreover, the high diversity of tree species in most tropical forests assures that individual feeding trees will on the whole be widely scattered. For example, Pries et al. (1953) found that the tree species of modal abundance in a *terra firme* forest in Brazil had a density of less than one individual per hectare. Thus the availability of suitable feeding trees to the bird species that habitually use them is by no means guaranteed.

The food supply in most feeding trees at the time of anthesis or ripening, as the case may be, is admittedly great. But as usage accumulates the amount of effort in searching that must be expended to procure a unit of nourishment will increase until the tree is no longer profitably exploitable. The period over which the remaining crop provides an adequate rate of feeding will depend on the intensity of usage. Exhaustion of the food supply in a feeding tree may often leave the local population without any equivalent alternatives. Thus when no feeding trees are available in the vicinity, many of the honey-eater species mentioned herein can be observed searching through foliage for insects, an occupation which yields food far less rapidly than the harvesting of feeding trees and which may not be sufficient when young are being fed. Even though food appears to be superabundant in most feeding trees, its current consumption can lead to scarcity at a later date when the supply has been exhausted. Hence the competition that at least potentially exists between the individuals and species that use a certain feeding tree must come as a result of the depletion of the standing crop and will be felt at a subsequent time, perhaps days or weeks after the tree received its heaviest use.

SPECIES-SPECIFIC BEHAVIORAL ATTRIBUTES AND THEIR RELEVANCE TO NICHE OVERLAP

The behavioral individuality of different species usually has the effect of lessening the niche overlap between them. Aggressive supplanting of one individual by another usually involved honeyeaters, most commonly, *Myzomela nigrita*, *Melidectes torquatus*, and *Xanthotis chrysotis*. The inherent aggressive tendencies of these species extended also to interspecific engagements. In the *Miarassa Ficus* quick aggressive responses of *Melidectes torquatus* towards *Melilestes megarhynchus*, *Pycnopygius cinereus* and *Melanocharis versteri* prevented individuals of these three species from using the tree for more than

a few moments at a time and seriously hampered their attempts to feed. In flowering trees at Karimui, *Xanthotis chrysotis* commonly displaced two other like-sized honeyeaters, *Xanthotis polygramma* and *Pycnopygius ixoides*, but reacted less frequently or not at all to the smaller *Meliphaga* spp. and *Oreornis obscurus*. In the Moluccas *Myzomela obscurus* supplants in flowering trees an equally small sunbird, *Nectarinia sericea* (Ripley, 1959). The apparent species-specificity of this type of behavior deserves further attention. The extent to which territoriality was involved in these interactions could not be ascertained, though very few collected individuals of these species were in breeding condition.

Specialized modes of feeding, even in trees that offer only one food source, can play a role in the competitive relations between species. The opening of *Ficus* fruits by parrots as a precondition for their further use by honeyeaters is a striking case in point. The possibilities in flowering trees are more numerous. Some species may concentrate on insects, others on nectar. In the white-flowered trees at Karimui we found that lorikeets (*Trichoglossus haematodus*) were actually feeding on the blossoms by biting off the receptacles and allowing the floral envelopes to fall to the ground. Destruction of flowers in a tree by one species palpably reduces its value to others that seek only nectar or insects.

Groups of birds using feeding trees cannot be considered flocks in the sense of socially integrated and temporally coherent units. For this reason we have chosen to use the word "assemblage" in connection with feeding trees, as discussed elsewhere (Diamond and Terborgh, 1967). Itinerant feeding flocks of the kind described extensively in the New World tropics by Davis (1946), Short (1961), Moynihan (1962), and in New Guinea by Archbold et al., (1942) do not exist at Karimui, though they occur in other parts of the island. Individuals and pairs of most species usually moved in and out of feeding trees independently of other members of the same species. Aside from the typically gregarious pigeons and parrots, movement in groups of more than two was noted only for *Gerygone chloronota*, *Mino dumontii*, *Oriolus szalayi*, *Gymnocorvus tristis*, *Diphylloides magnificus*, *Paradisaea apoda*, *Oedistoma pygmaeum*, and *Zosterops minor*. With the exceptions of *Mino dumontii* and *Oedistoma pygmaeum* these species were infrequent users of feeding trees. The random movements of both species and individuals to and from feeding trees in New Guinea had the effect of maintaining in them nearly constant or only gradually changing levels of usage for periods of several hours.

The realization that supplies of tree-borne foods in the tropics are sporadic and local provides a rationalization of the wandering and gregarious habits of such birds as those parrots and pigeons that obtain their livelihoods almost

exclusively from tree products. Selection for the efficient utilization of widely scattered concentrations of food would favor capabilities for sustained high speed flight and rapid harvesting of the available food. Gregarious behavior permits an increase in the proportion of the harvest that accrues to the members of a species. Furthermore, it is only by associating in flocks that individuals can be led to trees that have been located previously by other members of their species. Particularly in the case of large carpophagous pigeons we noticed that the birds often flew great distances and then on arrival in a suitable tree would satisfy their appetites in a few minutes. In view of this tendency, underestimation of the niche overlap between gregarious species is likely when observations span only one or two hours of the day. Though large birds show a greater character divergence in bill length among sympatric congeneric species than do small birds, suggesting reduced overlap in the size range of food taken (Schoener, 1965), we cannot yet assess this prediction in the light of field observations.

BEHAVIORAL STEREOTYPY

A few years ago Klopfer and MacArthur (1960) and Klopfer (1962) advanced the notion that tropical birds are more stereotyped in their behavior than temperate birds and that the corresponding contraction of niches may underlie the high diversity of species in the tropics. In support of this idea it was assumed that older bird taxa (non-passerines) would show greater behavioral stereotypy than newer taxa (passerines), and then shown that the proportion of non-passerine species in local faunas tends to increase towards the tropics. However, it is not generally acknowledged that older taxa invariably possess inferior adaptive qualities or lack behavioral versatility (Mayr, 1963). Experimental tests of these hypotheses have recently led Klopfer (1967) to the conclusion that behavioral stereotypy is more likely to be an effect rather than a cause of tropical diversity.

An inspection of the list of species that regularly feed on flowers in the Karimui region (Table 3) suggests that New Guinea birds are highly variable in at least two measures of behavioral stereotypy: vertical range of foraging in the vegetation and food spectrum. Moreover, the correlation between stereotypy and phylogenetic status is low. That the composition of this list is not peculiar to Karimui is indicated by Ripley's (1964) observations of *Xanthotis chrysotis* and *X. polygramma* along with two species of *Myzomela* and three species of *Charmosyna* lorikeets in a flowering tree in western New Guinea. Group I is composed of species that were found only in the upper branches of tall trees. Moreover these three species, all in the genus *Myzomela*, appeared only in flowering trees. Thus the *Myzomelas* are specialists (show stereotypy) on at least two counts: their range of vertical move-

ment is restricted and their feeding appears to be limited to flowers. The three species that occurred only in the lower strata of the forest (Group III) showed somewhat more diversified feeding behavior. *Macropygia* sp. and *Pycnopygius ixoides* fed both on flowers and small fruits, though *Zosterops minor* was attracted only to flowers. By far the largest number of species (8) fell into Group II, those that ranged widely through the vegetational column. In this group are two species, *Oedistoma pygmaeum* and *Toxorhamphus iliolophus*, that apparently feed only on flowers while the remainder visit two or more classes of feeding trees. Thus in the Karimui fauna it is possible to recognize species that are specialists both in their vertical movements and in the variety of food taken, species that are specialists in either one of these but not in the other and species that are generalists in both.

The phylogenetic status of the specialist and generalist species is opposite to the predictions of Klopfer (1962) though the small sample is hardly adequate to show a general trend. The four species that are restricted both in their vertical movements and in food preference (the three *Myzomelas* and *Zosterops minor*) are all passerines. On the other hand two of the four non-passerine species (*Charmosyna placentis* and *Trichoglossus haematodus*) are diversified both in their feeding and movements and a third (*Macropygia* sp.) feeds both on flowers and small fruit though is vertically restricted in its foraging. These results reveal clearly the difficulty of generalizing about behavioral sterotypy in tropical birds.

NICHE OVERLAP

The very spotty attention that has been given to feeding trees in the Neotropics suggests that the diversity of competitors there is at least as great as in New Guinea, if not more so. Alvarez del Toro in Chiapas, Mexico (fide, Eisenmann, 1964) observed a flowering vine, *Combretum farinosum* (*Combretaceae*), which attracted 69 species of birds within a span of 20 days. How many of these were actually feeding is not mentioned. Similarly, in observations that extended over a 2-month period. Land (1963) accrued a list of 57 species that appeared in or around a fruiting tree (*Miconia trinervia*) in the Caribbean forest of Guatemala. At least 20 species, including members of 11 families, were seen taking fruit. In Panama Eisenmann (1961) watched 16 species of 7 families hawking termites around a nuptial swarm and compiled a list of 22 species of 11 families that he saw feeding on *Cecropia* catkins in the clearing on Barro Colorado Island. A high ratio of families to species was also found by us (Diamond and Terborgh, 1967) in the bird assemblages at two fruiting trees in the Amazonian forest of Peru. During observations of about 4 hours at each tree we recorded 11 species of 9 families in one and 16 species of 10 families in the other.

These results taken together suggest that high levels of niche overlap in feeding trees are the rule in the Neotropics as well as in New Guinea. Of course it can be argued that it is the spectacular and perhaps atypical occurrences that get into print. However, in the course of many days spent searching for feeding trees in New Guinea we found that the majority of flowering and fruiting trees did not attract birds of any kind. Apparently their products were unpalatable. All trees that did consistently contain birds are described in this paper. Since the results from the more active New Guinea trees are comparable to those reported from the Neotropics, we may conclude that diverse feeding assemblages are not at all exceptional phenomena, either in New Guinea or in the New World tropics.

At Karimui a group of five honeyeaters (*Meliphaga* spp., *Xanthotis chryso-tis*, *X. polygramma*, *Oreornis obscurus*, and *Pycnopygius ixoides*) occurred together in most fruiting and flowering trees, usually in the order of abundance listed from greatest to least. This order is in complete accord with our impression of their relative abundances in the overall fauna, which suggests that all these species are opportunistic and use feeding trees of almost any sort whenever they are available. Because it was rare to see at one time more than five individuals of any of these species, it can be surmised that a suitable tree draws individuals only from the immediate vicinity. Aside from the tendency to concentrate their feeding activities at slightly different levels in the vegetational column, the mutual niche overlap among them appears to be extensive. Whether spatial differentiation of niches, as discussed by MacArthur (1964) accounts for the coexistence of so many generalists is an important question that cannot be resolved without further study.

The pattern of usage of different food sources could serve as an objective basis for the identification of ecologically homologous components in altitudinally or geographically isolated faunas. For instance, in the montane forests around Okapa (5,800 feet) there occurs a group of honeyeaters, including *Meliphaga orientalis*, *Melidectes torquatus*, *Melipotes fumigatus*, and *Pycnopygius cinereus*, all of which feed both on fruits and flowers. Considerable mutual niche overlap among these species suggests that collectively they are the ecological counterparts of the five Karimui honeyeaters that were the subject of the preceding paragraph.

Combined data from 13 New Guinea feeding trees that contained either flowers or small fruits indicates that the species of mean abundance in the trees accounts for 30 per cent or less of the total usage. Usage by species in other genera (67 per cent) and other families (46 per cent) comprises a far greater proportion. A comparison of these results with similar data from a temperate locality could provide a useful test of the postulate that niche overlap tends to be greater in the tropics.

SUMMARY

A widespread phenomenon in tropical forest is the gathering of varied assemblages of birds in trees bearing fruits, flowers, or some other plentiful food source. Repeated censuses of such feeding trees lead to a time-dependent measure of feeding for each species present. Results from 20 feeding trees in the New Guinea Highlands indicate the breadth of the food spectrum of many species and the extent of niche overlap between different species.

Honeyeaters and lorikeets accounted for more than 90 per cent of the use of each of 3 different species of flowers. Small fruits attracted more diverse assemblages comprising many families among which honeyeaters and pigeons predominated. Larger fruits were taken almost exclusively by pigeons.

Evidence is presented that niche overlap in feeding trees is reduced to some degree by species-specific behavioral attributes. These include aggressive supplanting of individuals and specialized feeding techniques. Many regular feeding tree users displayed marked tendencies to concentrate their activities at particular levels in the vegetational column.

From the point of view of the average avian user of feeding trees, 67 per cent of the tree usage is by species in other genera and 46 per cent by species in other families, indicating broad niche overlap. The range of feeding behavior displayed by different species did not correlate closely with phylogenetic status and varied greatly from restricted to diversified.

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AN APPRAISAL OF THE SONG OF THE BLACK-CAPPED CHICKADEE

KEITH L. DIXON AND RAYMOND A. STEFANSKI

THE songs of most species of birds are distinguished from call notes by the restriction of the former to one sex, and by the differences in the functions served by the two classes of sounds (Tinbergen, 1939:73-74; Thorpe, 1961:15). Song usually is confined to the mating season, and is associated with occupancy of a breeding territory. The vocalization considered to be the song of the Black-capped Chickadee (*Parus atricapillus*) often is transliterated as *fee-bee* or *phoebe*. The usual form is a sequence of two pure, whistle-like notes, the second lower in pitch (Fig. 1A). This vocalization is categorized as a song according to Tinbergen's definition ". . . those loud sounds that are given by birds of one sex especially at the beginning of the reproductive period." The restriction of loud singing to males during the breeding season, and the manner of delivery, as described by Bradford Torrey (quoted by Tyler, 1946), support this view.

In other respects this vocalization of the Black-capped Chickadee does not conform to the concept of "advertising" song as it is exemplified by other passerines. The *phoebe* song is not complex in its physical structure, as Bremond (1963) would require, and it is not delivered regularly from an exposed perch by males during the breeding season (Odum, 1941:327). These notes are not restricted to the breeding season (Bicknell, 1884:135; Saunders, 1947), and their functions may differ with the seasons. This unique song clearly warranted further study, some aspects of which we were able to pursue as a facet of a population study.

METHODS

Observations of behavior associated with singing were made in a population of color-banded chickadees whose nesting progress was known (Stefanski, 1967). Approximately 400 hours were spent in the field, principally in 1964 and 1965, in a deciduous woodland in the floor of Logan Canyon, 7 miles east of Logan, Cache Co., Utah, at an elevation of 5,000 feet. Some of the marked individuals were observed for short intervals in January and early February in a room 7 × 10 feet in area. After being conditioned to the room individually, they were confined by twos for a period of several days, and their behavior observed through simulated one-way glass windows. Vocalizations were recorded in the field and indoors with a Nagra IIIB tape recorder, and analyzed with a Kay Electric Company Sona-Graph. Playback experiments were conducted with breeding individuals of this population when the birds were known to be within hearing range. Either the playback system of the Nagra or a battery-powered amplifier-speaker system with a Transflyweight recorder was used. The tape recordings broadcast consisted either of songs or call notes of the flock integration ("chickadee dee") sort.

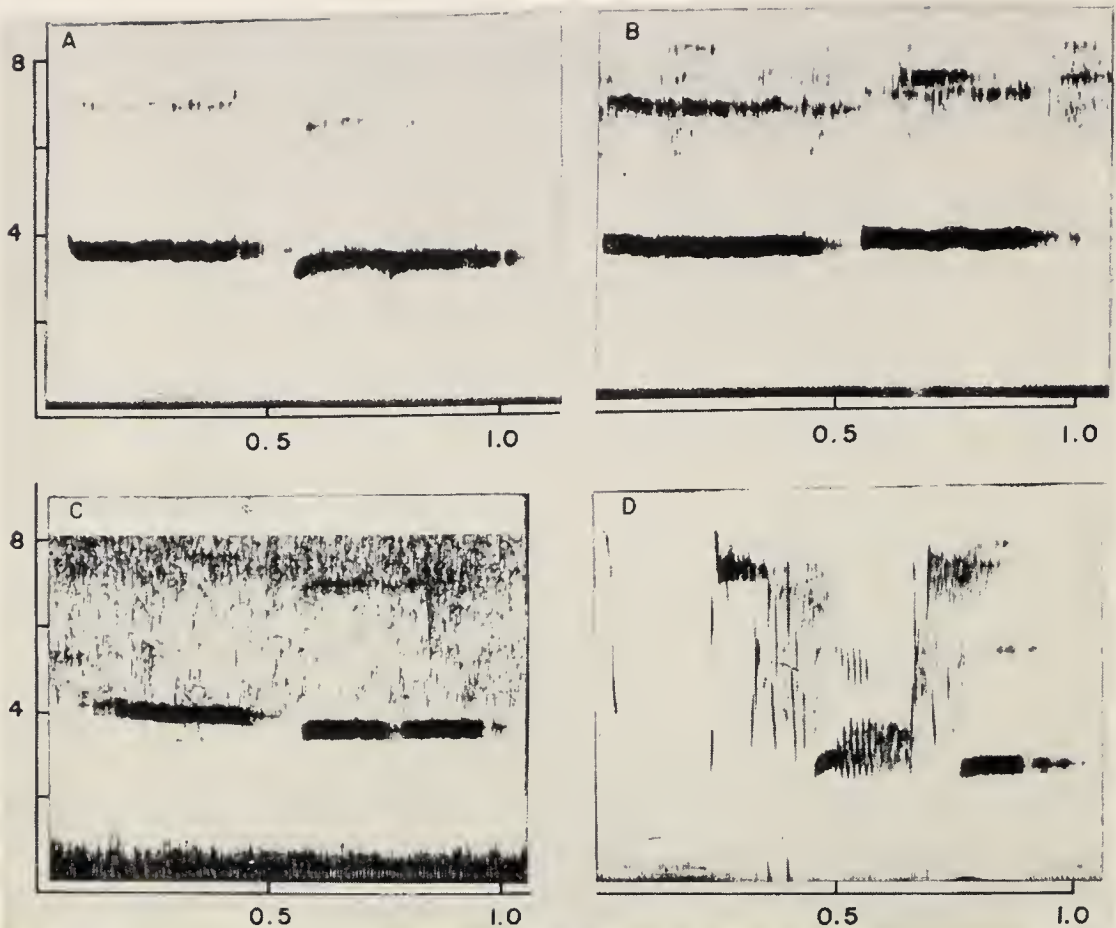


FIG. 1. Sound spectrographs of vocalizations of *Parus atricapillus*. Vertical scale, frequency in kilocycles per second; horizontal, time in seconds. A, typical song. B, song pattern with second note higher pitched. C, "signal" song of male approaching nest. D, fighting call uttered while supplanting a rival.

CONTEXTS OF SINGING BY MALES

The *phoebe* song is uttered infrequently in fall and winter, but the incidence increases with the weakening of flocking tendencies in early spring (Odum, 1941:322; Johnston, 1942). In late March and early April in northern Utah (the pre-nesting stage), exchanges of song occur in obvious relation to particular areas frequented by rival males. Most of these males already are paired. During this interval territorial boundaries are established, and these normally are altered only if the female selects a nest site outside the original territory.

Loud singing occupies a relatively small amount of the territory-holding male's time during the breeding cycle (Table 1). However, the higher incidence prior to incubation coincides with the maximum extent of breeding territory (Stefanski, 1967:Fig. 2), after which defended areas diminish in size. During this interval singing may begin without evident external stimulus.

TABLE 1
AN INDEX TO SEASONAL CHANGES IN INCIDENCE OF SINGING
OF BLACK-CAPPED CHICKADEES IN 1965

Stage:	Pre-nesting	Nest-building	Egg-laying	Incubation	Nestling
Inclusive dates:	27 Mch-15 Ap	16 Ap-17 My	18-25 My	26 My-8 Jn	9-29 Jn
Observer hours:	39	70	15	15	13
Incidence ¹	1.8	7.3	5.7	3.7	2.6

¹ Percentage of observer's time on a territory during which that particular male sang.

However, the sporadic nature of the singing and the size of territory occupied make it difficult to ascertain the circumstances of initiation in many instances.

Male Black-capped Chickadees exhibit a strong tendency to answer the songs of other males with song, and to approach singing rivals. The data presented in Table 2 reflect this disposition (singer approached in 18 of 26 incidents of categories 1A, B; and in all 11 experiments in which song was

TABLE 2
SUMMARY OF ENCOUNTERS OF BLACK-CAPPED CHICKADEES

I. Incidents initiated by distant detection of a singing rival	
A. Song exchanges by neighboring territorial males	17
1. singers remained in stationary positions	8
2. singers approached one another; confrontation ensued	9
B. Song not answered but singer was approached; skirmish followed	8
II. Contests initiated at close range	
A. Confrontations during which the intruder sang	11
1. defender responded with aggressive calls only	5
2. defender responded with song	3
3. defender evicted the intruder silently	3
B. Incidents in which the defender alone sang	2
III. Encounters involving pursuit or physical contact by combatants	28
A. Aggressive calls but no song uttered while contestants were sparring	26
B. Song uttered during skirmish	2
C. Singing occurred subsequent to clash	6
IV. Simulated violation of the territory	
A. Playback of flock integration calls	12
Defender perched above speaker and sang	9
B. Playback of song	11
Defender responded by singing while perched above speaker	11
V. Attacks on a trapped chickadee by a free-ranging individual (winter)	28
Number in which either participant sang	0

broadcast in the territory). In a pattern typical for the pre-nesting and nest-building stages, males approach one another while singing loudly and steadily, accompanied by their mates. They meet at a point on a common, tentative boundary and engage in a sparring match involving supplanting attacks and short pursuits of one another. Once visual contact is established as the birds are in proximity, song is replaced by a variety of sibilant, sputtery calls, one of which is illustrated in Fig. 1D. Following this sparring, which may involve the females also, the participants withdraw gradually. When no longer in proximity one or both males may sing, although this is infrequent (Table 2, III C). Such boundary contests are not always preceded by countersinging, but the delivery of song by one of the males usually is effective in precipitating a skirmish. Thus, singing does not repel an established rival, but rather serves to attract rivals to sites at which territorial boundaries are reaffirmed. The system of establishment and maintenance of territorial boundaries, then, does not involve distant vocal threat, and thus it differs from that of most songbirds.

The role of song in attracting males to the territorial boundary has not been emphasized previously, although Odum (1941:324) described loud singing as a part of the "challenge" and ". . . preceding the actual chase." However, the responsiveness of chickadees to imitations of their song is well known ("quickest summons in the bird world," according to Dawson, 1923: 610), and the broadcasting of song usually attracts a singing male to the site (Table 2, IV B). In most of the simulated intrusions the responding male appeared to be searching for the rival.

We noted singing during a territorial skirmish on only two occasions. Brewer (1961:365), referring to this species and to *P. carolinensis*, stated that ". . . if close distance conflicts take place, they appear about the same as fights at any other season." We infer from this statement that he did not note singing as part of the contest.

Unmated males.—Loud singing by male chickadees is heard upon the temporary disappearance of their mates, and males that are unmated sing much more persistently than do territory holders. They tend to wander randomly, and to intersperse among their songs some calls that ordinarily are delivered only during skirmishes. This latter response was noted infrequently in mated males in the absence of a rival.

Two males lost their mates in the course of this study. Both abandoned their territories and wandered widely, giving songs intermingled with "fighting calls." The male widowed at a later stage of the cycle (hatching) sang less frequently and continuously. When they were intruding, both males were intimidated easily but they usually resumed singing after being "escorted"

to the boundary. We witnessed the expulsion of a singing transient chickadee by a resident male as late as 30 June, a date when some broods have fledged.

On 11 and 12 May 1965, the singing of an unmated (but banded) male precipitated a clash between two territory-holding pairs, and the contest was renewed repeatedly upon the resumption of singing by the non-participant. On several subsequent occasions this unmated male ceased singing when answered by a territory holder. This unmated male remained in the vicinity, and nested nearby in each of the two following seasons.

Low-volume singing.—Song of low volume occurs in a variety of situations involving intrapair communication. One of these is the “signal” song uttered by the male as he approaches the nest in which the female is incubating or brooding. Spectrographs (Fig. 1C) support the structural identity of this utterance to the “territorial” song.

Males frequently deliver songs of moderate to loud volume in an apparent attempt to lead their fledglings away from a source of disturbance. One brood, 3 days out of the nest on 6 July 1964, flew 40 feet through dense willow growth to the source of broadcast of tape-recorded songs. (Odum's observation of subdued singing by both parents as the brood was leaving the nest cavity may be interpreted similarly.) On 15 July 1964, a male answered a song played back in his vicinity, and the fledglings (one week out of the nest) appeared agitated by the singing. The male retained his perch, and the response of the fledglings diminished.

Low-volume songs differ markedly in context from the “whisper songs” of parulids, such as *Dendroica kirtlandii* (Mayfield, 1960:127).

SINGING BY FEMALES

Singing by female Black-capped Chickadees has been reported by several authors (Dwight, 1897; Odum, 1942). It usually is of low volume, and we noted it only under unusual circumstances.

On two occasions a particular male interrupted his participation in the excavation of the nest cavity to fly to the boundary and begin singing. His challenge was not answered, and his mate approached, sang softly, and “led” him back to the cavity on both occasions.

A female whose mate was killed by a Sharp-shinned Hawk (*Accipiter striatus*) on 6 April 1965, sang intermittently for several hours thereafter.

In one case, in which the brood was divided between the two parents, the female (known to be in her third breeding season) sang to lead the brood. Such singing by the female was not noted when both parents remained with the brood. In the following year this female's new mate, a second-year male, was not notably aggressive, and this female sang steadily at the territory boundary for 7 minutes. Her mate did not sing during this interval, and

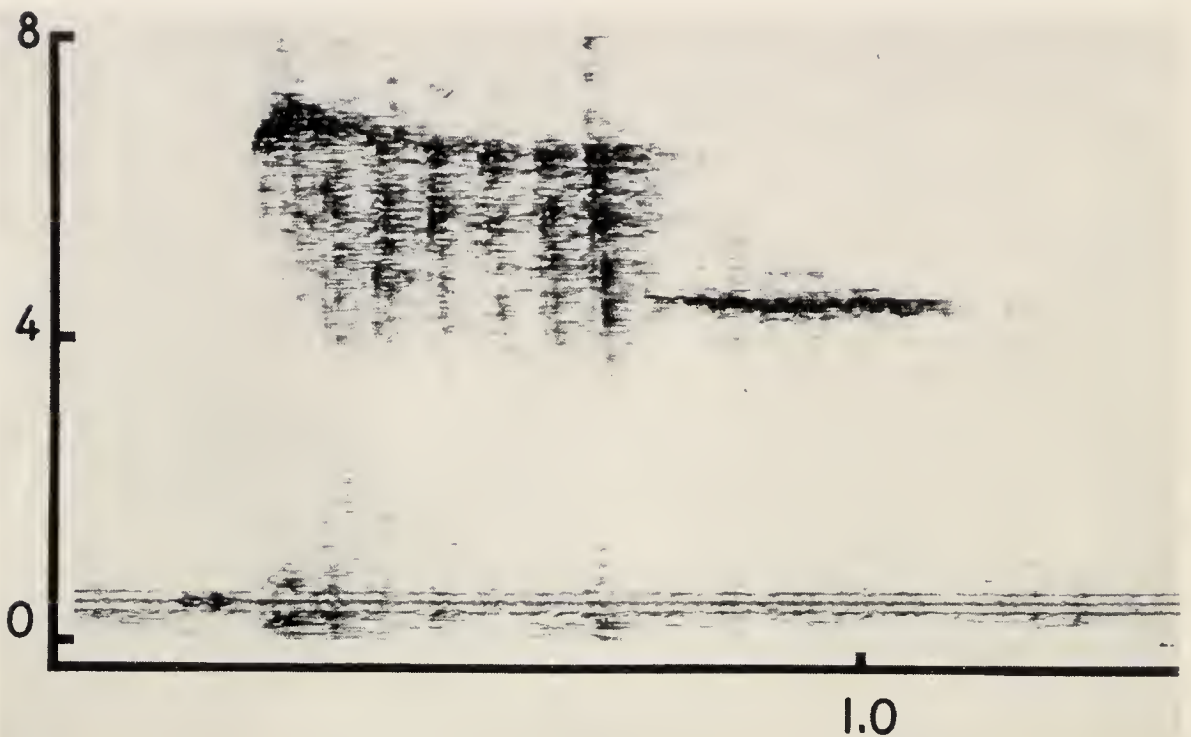


FIG. 2. "Chatter-fec" sequence uttered by a captive Black-capped Chickadee following separation from a social companion.

the "challenge" was not answered by any neighboring male. One female, known to be in her second nesting season, sang on several occasions in the temporary absence of her mate, and even answered his song softly at times during the nest-building and egg-laying stages. Another female delivered a "signal" song while approaching the nest 10 days after hatching. Thus, singing by females normally serves in intrapair or parent-offspring signalling.

OBSERVATIONS OF CAPTIVES

After two captive chickadees had been confined together in an observation room for one and one-half days or longer, a single-cell wire trap was placed on the floor. The member of the "couple" that was trapped effectively "disappeared," and the other bird usually paid little or no attention to the trap. Soon after the male of one couple was so trapped on 31 January his female companion, which had dominated him for the five days of their association, uttered a "chatter" similar to that denoting "disturbance" in other contexts, then a song note (Fig. 2). Similar sequences of softly-uttered song notes in a separation context were given by two males on 4 occasions when their partners were trapped or removed from the room. One female gave such a sequence twice, and a bird of undetermined sex did so once. The males sang at the "disappearance" of both male and female partners, and the female uttered song notes following the removal of both male and

female companions. On two other occasions females were silent and otherwise appeared unperturbed.

Although the absence of the mate has been suggested as a proximate cause for singing in many passerines (Andrew, 1961), three aspects of these observations of captives seem noteworthy. These are the short duration of acquaintance, the mid-winter condition, and the either-sex relationship.

DISCUSSION

Whether loudly or softly uttered, the song notes or *phoebe* whistles of Black-capped Chickadees serve as signals that function in attracting the recipient to the vicinity of the signaller. This "beckoning" function appears in the close-quarters intrapair signalling of either male or female (leading the mate to or from the nest, leading the brood, attraction of neighbors to a common territorial boundary). Even in the last context the mate as well as the rival may be "beckoned," thus facilitating defense of mate.

With the onset of the breeding season loud singing becomes associated with particular sites (although song is not delivered from an exposed perch). The possession of and tendency to defend an area is evident in the use of song by the territory holder in 20 of 23 simulated intrusions (Table 2, IV A, B). Further, the proclivity to answer the songs of other individuals is characteristic of this season. Possibly the "awakening song" (see Davis, 1958:327) serves also in the announcement of occupancy. However, "concern" with general area rather than precise territorial boundaries seems evident from our observations and those of Odum (1942:526).

The use of the *phoebe* notes by male and female in separation context, as "signal" song, and in leading the mate or brood, suggest the origin of this song as an intrapair signal, denoting a particular social relationship. The essential restriction of loud singing to breeding males, and in relation to occupancy of a particular area, suggest that the original intrapair signal was enhanced under hormonal influence. The disposition to *answer* a rival doubtless reflects a lowering of a threshold for aggression facilitated by androgens (see Marler and Hamilton, 1966:175). Although accompanied by ". . . a tendency for dominance to be linked with environmental references such as a territory" (Marler and Hamilton, loc. cit.), the song exchange in *Parus atricapillus* does not express as high a level of aggression as that found in boundary skirmishes.

The *phoebe* song seems to function as a means of locating the rival, challenging and beckoning him to a meeting site rather than as a means of repelling him from a fixed boundary. Individual recognition probably plays a role in such contests. For example, in the encounters observed on 11 and 12 May 1965, the mated territory holders clashed with one another, virtually ignoring

the unmated male whose singing had precipitated the contest. This specialized system of *atricapillus* relates to the transitory territorial boundaries (Stefanski, 1967) and to "sexual" territory (Odum, 1941:326), seasonally more extended than in Odum's original view. In the latter interpretation (defense of mate by confrontation rather than indirectly by the maintenance of precise boundaries), Mrs. Louise deK. Lawrence concurs (pers. comm., 1967). Thus the song of the Black-capped Chickadee does not serve as a distant threat or as a substitute for fighting as do the songs of most passerines (Thorpe, 1961:43). In view of the postulated origin from contact calls rather than threat notes, and the unique territorial system of this species, these differences in function are not unexpected.

The proximate cause of singing in this species is not clear. In some situations (temporary separation, dawn singing) absence of the mate is the evident external stimulus. Immediately following a skirmish the withdrawal of the rival from the boundary may evoke singing, a point noted for *Parus major* by Hinde (1952:68), and for some other passerines by Andrew (1961:552). On several occasions during the nest-building phase we gained the impression that the males were "seeking" song exchange. Incidents such as that described under "Singing by Females" did not seem to represent a carryover from previous boundary confrontations. If the song were answered the initiator often was brought into a different stimulus situation, a skirmish in which further singing was replaced by more complex vocalizations reflecting stronger attack tendencies (see Fig. 1D).

A similar conclusion was reached for the Chaffinch (*Fringilla coelebs*) by Marler (1956:88). He stated that ". . . as soon as the conflict increases song stops" . . . and that ". . . it seems that song only accompanies the mildest tendency to attack." In these two species, then, song does not appear strongly aggressive in nature. However, in some other passerines, such as the Song Sparrow (*Melospiza melodia*) (Nice, 1943:154-156; J. A. Mulligan, pers. comm.), the American Robin (*Turdus migratorius*) (Young, 1951), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Davis, 1958:317), low-volume, rapidly uttered versions of advertising song motifs are uttered during confrontations. Further, in the Plain Titmouse (*Parus inornatus*) (Dixon, 1949:117, 1969:96), singing may occur in the course of fighting, and may be directed at trapped conspecifics that are being attacked. In contrast (Table 2, IIIA, V) "fighting" calls rather than *phoebe* songs are uttered by Black-capped Chickadees in such skirmishes and attacks. Thus among the passerines there appear marked differences in the relationship of advertising song motifs to the threat or fighting calls that are uttered during confrontations.

Presumably the acoustic properties of the pure tones of intermediate

frequency (Fig. 1 A-C) are better suited to transmission in the dense swamp woodlands inhabited by many populations of this chickadee than are the fighting calls of varying frequency (see Marler, 1955:6). Hence the *phoebe* whistle has been enhanced as a distant signal denoting occupancy of an area, but the original valence in evoking an approach to the signaller has persisted.

SUMMARY

The contexts of singing were studied in a population of marked individuals of *Parus atricapillus*, and in short-term captives confined as couples. Exchange of the "whistled" song attracts rivals to a common boundary where a skirmish, accompanied by calls of varying frequency, may occur. Thus the song attracts rivals rather than repelling them. Songs of low volume are uttered by males when approaching the nest and when leading the mate or fledglings. Females sing softly in similar contexts of intrapair signalling. Captives of either sex delivered primitive song notes when separated from a partner of a few days' acquaintance.

In most contexts song seems to function as a summons. The origin appears to be from an intrapair signal enhanced by hormonal influence, and related to occupancy of an area. This song is not as indicative of a tendency to attack as are the fighting calls of varying frequency. The *phoebe* song does not function as a distant threat, and relates more to the defense of the mate than to defense of fixed boundaries. The structure of this song is such that it may be detected in dense woodlands at greater distances than the fighting calls.

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ANNOUNCEMENT

A symposium, "Distributional History of the Biota of the Southern Appalachians: Part 3, Vertebrates" is scheduled to be held at Virginia Polytechnic Institute, 25-27 June 1970, and will include the discussion of birds. Those interested may write for a program to: Jerry Hargis, Continuing Education Center, VPI, Blacksburg, Virginia 24061.

STATUS AND SPECIATION IN THE MEXICAN DUCK (*ANAS DIAZI*)

JOHN W. ALDRICH AND KENARD P. BAER

THE basis for listing animal populations as in danger of extinction by both the U.S. Bureau of Sport Fisheries and Wildlife (1966) and the International Union for Conservation of Nature and Natural Resources (1966) is the currently accepted name of the species and subspecies taxonomic units. Inclusion of the subspecies, as well as the species, category permits the designation of many endangered populations that are in need of protection but which are conspecific with nonendangered ones. This also simplifies the problem of singling out for protection, populations such as the various endangered mallard-like ducks about which currently there is no agreement as to whether they should be considered subspecies of the Mallard or distinct species. The Mexican Duck (*Anas diazi*) is one of these.

There is the further problem of deciding whether the Mexican Duck itself is divisible into subspecies. For many years, the northern population of the Mexican Duck has been listed in standard references such as J. C. Phillips (1923), Peters (1931), Friedmann, Griscom, and Moore (1950), and American Ornithologists' Union (1957) as a distinct subspecies (*A. d. novimexicana*), although other authors, notably Hellmayr and Conover (1948), Delacour (1956), A. Phillips (1959) and Johnsgard (1961*a* and *b*) have considered this distinction unwarranted. Up to the present, no adequate analysis seems to have been made of the presumed characters separating the two. If *novimexicana* is a valid taxon, it is indeed in danger of extinction, although there is some question as to whether the species, *Anas diazi*, as a whole, is threatened. Since the priority of attention these ducks receive at the hands of wildlife managers depends on the status of specific recognized taxa, sound conclusions on their taxonomy are imperative.

OBJECTIVES

One of the purposes of the present study was to investigate the differences in the Mexican Duck populations to see if there is evidence for racially distinct groups. Another was evaluation of the taxonomic relationship of *Anas diazi* to the Mallard (*Anas platyrhynchos*). A third objective was to obtain current information on the distribution, abundance, and factors affecting survival of the various populations currently included under the name, *Anas diazi*.

PROCEDURES

Study of geographic variation of *Anas diazi* and morphological phases of its relationship to *platyrhynchos* was by comparison of specimens in the U. S. National Museum

supplemented by specimens borrowed from other museums. Specimens were compared in series on a large table in the Division of Birds of the U.S. National Museum under a Maebeth Examolite Fixture, Type TC440, a combination of artificial lights designed to simulate daylight quality. Determination of the characters of populations was based on adult specimens separated by sex and season. Specimens taken during the arbitrarily delimited breeding season (25 April through August) based on egg dates (Bent, 1923 and Lindsey, 1946) were segregated for comparison separately. This was considered necessary because even though the species is generally considered sedentary (Leopold, 1959), there is a probability of significant movement of populations during the nonbreeding season (Johnsgard, 1961*a*). Since a paucity of "breeding season" specimens was found in collections, additional birds were collected by the authors in Mexico during May 1966.

Study of morphological distinction from the Mallard was by direct comparison of specimens. To obtain information on current distribution and abundance, Baer searched for the species by ground and air surveys in Chihuahua and New Mexico in 1964 and 1965, and both authors examined most of the Mexican portion of the range by ground surveys in May 1966.

DISTRIBUTION AND STATUS

The original breeding distribution of the Mexican Duck extended from extreme southeastern Arizona (Gila River drainage) and central northern New Mexico (Rio Arriba County) southward in the Rio Grande Valley in New Mexico through central western Texas (near El Paso) and the Mexican highlands to the Trans-Mexican Volcanic Belt (as defined by Dickerman, 1963) from Jalisco and Nayarit east to Puebla (Leopold, 1959).

To a large extent, the Mexican Duck has disappeared as a breeding species from the avifauna of the United States. As far as known, it now breeds only locally along the Rio Grande and in extreme southwestern New Mexico and southeastern Arizona. Most areas where it formerly bred within the United States have been drained or otherwise disturbed to the extent they are no longer suitable habitat. Efforts are being made to redevelop suitable Mexican Duck breeding habitat at the La Joya State Game Management Area and the Bosque del Apache National Wildlife Refuge, both on the Rio Grande in Socorro County, New Mexico; also the San Simon Cienega, controlled by the Bureau of Land Management, in Hidalgo County, New Mexico, and adjoining section of Arizona. Although the Mexican Duck has been found in the past in Texas along the Rio Grande near El Paso, there are no definite records of nesting within that state. Charles Heumier (pers. comm.) is sure a few birds nest near Indian Hot Springs on the Rio Grande in Hudspeth County. He banded an immature male near the community of Lobo, 15 miles south of Van Horn, Texas, and reported that 35 were seen on the 1967-68 Christmas Bird Count on Balmorhea Lake, south of Pecos. These Texas localities, a marsh on the Gray's Ranch, 30 miles south of Animas in southwestern New Mexico and the La Joya and Bosque del Apache Refuge areas seem to be the only places where Mexican Ducks have

been found in a wild condition recently in the United States. Twenty of these birds were observed at Gray's Ranch from an airplane by Baer and Wellein on 2 November 1964, and four pairs, also from the air, on 3 May 1965. Other areas with potential Mexican Duck habitat noted on recent surveys in southwestern New Mexico and adjoining Chihuahua are the Slaughter Ranch on the international boundary in southwestern New Mexico, and Mimbres Lake about 14 miles west of Las Palomas, Chihuahua. In January 1965, Baer estimated at least 1,000 Mexican Ducks in a mountain valley lake in the vicinity of Babicora, central-western Chihuahua and collected three specimens, whereas in May 1966, our 2-day search in this area produced only one pair on the almost dried-up lake. Lago Babicora was reported to be completely full again in the winter of 1967-68, showing the great fluctuation in water level which takes place in this lake. Presence of Mexican Ducks in such lakes during the winter is no indication that they will nest there.

Our survey in Mexico during May 1966 indicated that the Mexican Duck is still present in small numbers and widely scattered in much of its former range during the breeding season; but sinks and potholes, which formerly produced much of the suitable habitat, are gone or are rapidly drying up because of overgrazing, drainage for farming, or diversion of water for human needs as pointed out by Leopold (1959) and Dickerman (1963). Much of the habitat today persists along rivers with copious flows of water such as the Conchos in Chihuahua, and around artificial impoundments or presas. The latter, however, are unreliable because of draw-down of waters in dry periods.

Johnsgard (1961a) has mapped the complete range of the Mexican Duck based on both specimens and acceptable sight records. His map (p. 4) agrees with the map of Leopold (1959, p. 173) in indicating an unbroken range between "New Mexican" (northern) and "Mexican" (southern duck populations). Actually, both maps show a rather wide break between records in central Chihuahua and those in central Durango; also one between the latter localities and the next records to the south in southern Nayarit and Aguascalientes. Although our May 1966 sight records for southern Chihuahua and southern Durango (cited beyond) narrowed these gaps somewhat, our observations tended to substantiate the impression that there are rather wide gaps in the distribution of this species in northern Mexico generally, probably chiefly as a result of scarcity of suitable habitat in those areas.

On the other hand, this is equally true of our experience in the southern part of the range of the Mexican Duck in the Trans-Mexican Volcanic Belt, considered by Leopold (1959) to be the center of abundance of the species. Actually, we found them at fewer localities in this area in May 1966, despite

more potential habitat, than we did further north. Large populations of people and livestock around water in this region could be a reason for scarcity of ducks. One area near Lake Chapala and another in Tlaxcala were the only ones where Mexican Ducks were noted south of the northern Jalisco area near Aguascalientes. However, in his much more intensive observation of nesting marshbirds in relatively recent years, Robert Dickerman (pers. comm.) found five Mexican Ducks on 2 August 1957 at Laguna Magdalena, Jalisco; a family of eight downy young (5 collected), 3 August 1957, at Lago Chapala, Jalisco; a pair with downy young, 10 July 1957, and three families plus many others seen, three downy young collected, 12 July; one adult collected 10 July 1957, at Laguna del Carmen, Puebla; 10-15 birds and a nest with 4 eggs, 8 July 1958, north of Maravatio, Michoacan; 20+ birds, 24-25 May 1961, at Laguna San Pedro Lagunillas, Nayarit. The extensive marshes near Lerma in the Toluca Valley, State of Mexico, which E. A. Goldman (1951) and George B. Saunders (pers. comm.) considered an important breeding area for the Mexican Duck in former times, and where Robert Dickerman has seen them in recent years, are practically gone and we saw none of this species there in 1966.

Earlier impressions of greater abundance of this species in more southern portions of its range may possibly have resulted in part from the concept that the species was essentially sedentary (Leopold, 1959) and that concentrations in that area of migrants or wandering birds from more northern areas during the nonbreeding season were actually a permanent population. That large concentrations of these ducks still do winter on some of the southern lakes is indicated by the record of at least 1,000 seen on a lake between Ahaluco and San Juanito, Jalisco, 21 and 22 January 1968, by Lytle Blankenship (pers. comm.). It would seem that so many birds must have congregated from a rather extensive breeding area, thereby supporting the idea of partial migration (Johnsgard, 1961a).

Localities, dates, and numbers of Mexican Ducks observed and collected by the authors in 1966 were: Lago Babicora, Chihuahua, small pond, 7 May, 2 (1 pair); Ciudad Guerrero, Chihuahua, small pond, 7 May, 4 (1 pair); Julimes, Chihuahua, Conchos River, 9 May, 6 (3 pairs); Julimes, Chihuahua, Conchos River, 27 May, 1 duck (2 nests with eggs found between 9 and 27 May reported to us); Boquilla, Chihuahua, Conchos River, 10 May, 6 (3 pairs); Parral, Chihuahua, lake south of town, 11 May, 1 duck; Ciudad Durango, Durango, lake 20 mi. north of city, 11 and 12 May, 4 (2 pairs); Ciudad Durango, Durango, lake 40 mi. southeast of city, 12 May, 6 (3 pairs); Jalisco, small lake 30 mi. south of Ciudad Aguascalientes, 13 May, 6 (3 pairs), 1 duck collected; Jalisco, small lake 30 mi. south of Ciudad Aguascalientes, 14 May, 15 ducks, 2 collected; Jalisco, small lake 30 mi. south of Ciudad Aguascalientes, 25 May, 12 (6 pairs), 1 duck collected; Jalisco, 3 small ponds 23 mi. south of Ciudad Aguascalientes, 25 May, 6 (3 pairs), 2 ducks collected; Jalisco, 3 small ponds 20 mi. southwest of Ciudad Aguascalientes, 25 May, 25 ducks, 3 collected; Jalisco, pond 50 mi. south of Ciudad Aguascalientes, 15

May, 2 (1 pair); Ciudad Tlaxcala, Tlaxcala, lake east of city, 19 May, 7 (3 pairs); Ciudad Tlaxcala, lake east of city, 18 May, 6 (3 pairs); Chapala, Jalisco, 6 mi. northwest, small pond, 23 May, 8 (4 pairs), 1 duck collected; Chapala, Jalisco, 6 mi. northwest, small pond, 24 May, 16 ducks; Las Delicias, Chihuahua, large lake, 28 May, 2 (1 pair); Las Delicias, Chihuahua, large lake, 29 May, 2 (lone), 1 collected; Las Delicias, Chihuahua, canal, 29 May, 17 (1 hen with 4 ducklings), 1 adult collected.

Localities in northern Jalisco south of Ciudad Aguascalientes and along the Rio Conchos and its tributaries in east-central Chihuahua were the most productive of records. The two nests with eggs found between 9 and 27 May at Julimes, Chihuahua, were reported to us by Señor Manuel Ramirez, former mayor of the town, whose observations were known by Baer to be reliable. The brood at Las Delicias, Chihuahua was found by Baer. These were the only places where we had definite evidence of Mexican Ducks nesting. In fact, in most other places, the occurrence of both members of the pair together at all hours of the day, and the incompletely developed gonads of specimens collected indicated that nesting had not started. It may be that nesting is delayed, as suggested by both Allan Phillips and Robert Dickerman (pers. comm.), until the beginning of the summer rains. Exceptions to this are especially favorable localities such as we noted along rivers and canals with a permanent and copious flow of water. The beginning of egg laying by captive Mexican Ducks in early April at the Bosque del Apache Refuge, New Mexico, where water is supplied artificially, but summer rains do not normally come until June or July, tends to support this theory. Although there are a few records of April and May nesting in New Mexico (Lindsey, 1946), initiation of egg-laying for the most part, both in that area and further south, appears from records of eggs and downy young to be after the first of June.

In all, 120 Mexican Ducks were seen in 14 of the 43 likely areas inspected in Mexico between 6 and 29 May 1966. Of these, 12 (7 males and 5 females) were collected. This seems like a very small and scattered population considering the distance traveled and special efforts to find these birds. This, together with the shortage of water in general and the disturbance of habitat by people and livestock almost everywhere, indicates that the survival of this species may be endangered.

MORPHOLOGICAL VARIATION

Viewed in series and individually from above, male Mexican Duck specimens of all seasonal and geographic groups showed a more pearly-gray wash on the tertials than females. Below, males showed a generally darker appearance, particularly on the chest, which was also more reddish brown. Several

males from New Mexico and Chihuahua showed traces of Mallard characteristics. This took the form of varying amounts of green on the head and vermiculation on the dorsal plumage.

The presence of varying amounts of bright yellow on the bills of four males and one female from New Mexico and northern Chihuahua is not understood. No specimen from the southern part of the range of *Anas diazi* showed this characteristic and only one out of many specimens of *Anas platyrhynchos* examined, a male from the State of Washington, showed a similar condition.

Breeding specimens (late April through August) differed from those taken at most other times of the year only in appearing slightly more worn in most birds. However, September specimens were the most worn of all.

Specimens of both sexes from south of Chihuahua, generally referred to as *Anas diazi diazi* (American Ornithologists' Union, 1957; and Friedmann, Griscom and Moore, 1950) appeared very similar to birds from Chihuahua northward, generally considered as representing *A. d. novimexicana*. Viewed in series, the southern specimens averaged very slightly darker and more brownish, less grayish, with feather edgings more rufescent, and less buffy below. This was due to an average darker color of light buffy portions of the feathers of the underparts and more heavy streaking of brown. When only specimens taken during the arbitrarily designated breeding season were included, the series was less variable and the differences between northern and southern groups slightly more pronounced. The differences were more pronounced in the males in which southern specimens were darker particularly on the posterior underparts and had less reddish brown chests. Pitelka (1948) noted similar differences in specimens available to him which were also used in the present study. As Pitelka pointed out, the irregular wavy barring of fulvous on the mantle, mentioned as a character of a northern form by previous investigators, is found in certain individuals in all populations and is of no taxonomic significance.

An effort was made to exclude all specimens which showed indication of hybridization with the Mallard from the series used for study of geographic variation. However, there is a possibility that the more grayish and paler coloration noted in the northern group resulted from infiltration of Mallard genes without resulting in obvious Mallard characteristics. In any case, the average color differences between northern and southern populations are too slight and individual differences in each series too great to permit identification of single birds as of northern or southern type. Furthermore, there appears to be virtually no difference in size, indicated by the following measurements, which would be of use in distinguishing these populations.

Northern specimens, *A. d. novimexicana* (?), all seasons

Adult Male (18 specimens): Wing, 260–289 (273.9) mm; tail, 75.4–90.7 (85.1); exposed culmen, 50.4–56.4 (53.0); tarsus, 40.1–47.4 (44.2); mid-toe without claw, 47.8–58.2 (52.0).

Adult Female (27 specimens): Wing, 237–271 (254.7) mm; tail, 68.1–88.6 (81.7); exposed culmen, 47.1–55.1 (51.0); tarsus, 38.3–49.3 (42.6); mid-toe without claw, 46.7–58.4 (51.7).

Southern specimens, *A. d. diazi* (?), all seasons

Adult Male (13 specimens): Wing, 260–282 (269.9) mm; tail, 76.0–95.0 (86.3); exposed culmen, 51.1–55.6 (53.3); tarsus, 43.1–48.4 (46.3); mid-toe without claw, 51.4–57.7 (53.7).

Adult Female (13 specimens): Wing, 232–268 (253.4) mm; tail, 80.0–89.5 (85.1); exposed culmen, 45.5–52.7 (50.3); tarsus 40.2–43.6 (42.0); mid-toe without claw, 47.3–53.1 (49.8).

Northern specimens, *A. d. novimexicana*, breeding season

Adult Male (5 specimens): Wing, 272–289 (278.4) mm; tail, 78.1–90.4 (84.1); exposed culmen, 51.6–56.4 (53.5); tarsus, 42.2–47.4 (45.0); mid-toe without claw, 50.3–54.1 (52.1).

Adult Female (13 specimens): Wing, 242–271 (254.4) mm; tail, 77.2–88.6 (82.6); exposed culmen, 47.1–55.1 (50.7); tarsus, 38.3–49.3 (42.8); mid-toe without claw, 46.7–58.4 (52.2).

Southern specimens, *A. d. diazi*, breeding season

Adult Male (10 specimens): Wing, 260–282 (269.1) mm; tail, 76.0–95.0 (86.0); exposed culmen, 51.1–55.6 (53.2); tarsus, 43.1–48.1 (46.0); mid-toe without claw, 51.4–55.1 (53.2).

Adult Female (13 specimens): Wing, 232–268 (253.4) mm; tail, 80.0–89.5 (85.1); exposed culmen, 45.5–52.7 (50.3); tarsus, 40.2–43.6 (42.0); mid-toe without claw, 47.3–53.1 (49.8).

In view of the lack of difference in either color or size that would make it possible to identify reliably a specimen as representing either northern or southern populations, we conclude that the "New Mexican Duck," *Anas diazi novimexicana*, is not a valid subspecies and that the Mexican Duck is a monotypic species.

RELATIONSHIP TO THE MALLARD

The large number of specimens in collections which show morphological evidence of mixture of genes of *Anas diazi* and *Anas platyrhynchos* raises a question as to the specific relationship of the two. Lindsey (1946) and William Huey (pers. comm.) give evidence that individuals with mixed characteristics may be of fairly common occurrence. Lindsey noted that hybrids usually outnumber the pure Mexican Ducks wintering in Rio Grande Park, Albuquerque, New Mexico. Huey considers this situation abnormal because those ponds, which were associated with the Albuquerque Zoo, usually contained a mixture of domestic mallard-type birds. He says that among ducks trapped for banding at the State refuge at Radium Springs, New Mexico,

ratios of what were considered pure bred to hybrids were: 1959, 20/6; 1960, 15/11; and 1961, 23/11. There is no way of relating these figures to the proportion of hybrids to purebreds of either Mexican Ducks or Mallards in any given breeding population.

Opinions of systematists differ on how to handle this situation in the nomenclature. Nomenclatural treatments, such as Peters (1931), Hellmayr and Conover (1948), Friedmann, Griscom, and Moore (1950), and American Ornithologists' Union (1957), accord Mallards and Mexican Ducks distinct species rank while Delacour (1956), A. Phillips (1959, 1961), and Johnsgard (1961*a, b*) consider them conspecific. The difference of opinion is probably largely the result of differences in concept of what constitutes a species. The mere fact that hybridization occurs, of course, is not enough to deny specific rank. Practically all species of ducks will hybridize, especially if mates of their own species are unavailable. This happens frequently in captivity but rarely in the wild. The criterion we are following is that two populations are considered as distinct species if they do not ordinarily interbreed when they come together in the wild. It would appear that the Mexican Duck and the Mallard do interbreed when they come together in the wild, but there is still a question of the extent to which this occurs—whether it is the rule or the exception. Unfortunately, both Mexican Ducks and Mallards are so rare where they occur together during the breeding season that it is difficult to determine the incidence of their interbreeding. This rarity in itself results in a shortage of mates of the same type and is thus conducive to crossing with one of the other type. There is no doubt that we have here a borderline situation between species and racial status.

It seems likely that the sexually monomorphic Mexican Duck, like the Black Duck (*Anas rubripes*) differentiated from the wide-ranging dimorphic common Mallard in the past as a result of ecological or distance barriers to gene flow and different sets of selection factors as postulated by Johnsgard (1961*a*). In more recent times, this reproductive isolation appears to be breaking down, possibly due to man-induced habitat changes. As a result of these secondary junctions, hybridization of both Mexican and Black Ducks with Mallards is taking place. Whether this process progresses to the complete genetic amalgamation of the overlapping populations depends on the extent to which reproductive barriers have evolved during the periods of isolation. In the case of the Mexican Duck, factors possibly inhibiting, if not actually preventing crossing with Mallards, might be their lack of sexual dimorphism which would guide the female in choosing a mate of her own kind, different nesting habitat requirements, different climatic tolerance and different timing of reproductive condition based on rainfall cycles. Mallard and Mexican Ducks resemble one another chiefly in female plumage, but even in this there

are some rather distinct differences as indicated in detail by Huey (1961).

In assessing the species relationships of North American mallard-like ducks, Johnsgard (1961a), after detailed analytical studies, concluded that none of the described plumage or soft part characters, aside from sexual dimorphism of *platyrhynchos*, were of absolute diagnostic value. Our much less detailed studies of plumage and soft parts agreed with his findings. Johnsgard noted that experimental breeding had shown that the genetic basis for sexual dimorphism in the Mallard is relatively simple and not sufficient to be considered as a basis for a species difference. No qualitative, only quantitative, differences were noted in courtship displays between Black Ducks and Mallards. This quantitative difference in behavior of Black Duck was thought possibly to compensate for lack of sexual plumage differentiation in mate selection. However, courting groups of the species normally remained almost completely segregated and hybrids tended to court with groups they most closely resembled. No observations of sexual behavior of Mexican Ducks were obtained but Johnsgard's notes on the Black Duck and Mallard are strongly reminiscent of Huber's (1923) observation that while flocking in winter and early spring, Mexican Ducks stayed together and did not mix with Mallards. Johnsgard (1963:538) concluded that it appears that isolating mechanisms in *Anas* are based primarily on male plumage or soft part features and associated courtship displays that exhibit these features. Still later, Johnsgard (1967:61) found that obvious Mallard \times Black Duck hybrids rarely exceed more than 2 per cent of combined populations indicating that assortive mating is operating effectively. Although similar data are unavailable for the incidence of Mallard \times Mexican Duck hybrids, if the assortive mating is due largely to the great difference in plumage pattern and color of the males, one might expect a similar incidence of mating inhibition between Mexican Ducks and Mallards as between Black Ducks and Mallards.

Only time and further study will show to what extent speciation has progressed in the case of the Mexican Duck. However, until it is demonstrated that the sexually monomorphic *diazi* and dimorphic *platyrhynchos* populations are freely interbreeding, and ducks of hybrid type definitely outnumber examples of apparently pure strains in breeding areas in the zone of contact, it would seem advisable to follow the concept of two distinct but closely related species, *Anas diazi* and *Anas platyrhynchos*. This concept would seem to agree with that of the semi-species as elucidated by Short (1969) who also thought these units should be considered taxonomically as species.

SUMMARY

1. Currently recognized northern and southern subspecies of the Mexican Duck are not based on sufficiently distinct or consistent size or color characters to be maintained. Therefore, the species is considered monotypic.

2. Although a borderline case in species distinctness, the Mexican Duck (*Anas diazi*) appears to have a certain amount of reproductive isolation from the Mallard (*Anas platyrhynchos*) in areas of sympatry. Therefore, it is considered as taxonomically a distinct species.

3. The Mexican Duck has virtually the same overall geographic distribution now as formerly which is southeastern Arizona, the Rio Grande Valley of New Mexico, and central-western Texas southward through the central highlands of Mexico to the Trans-Mexican Volcanic Belt south of Mexico City. However, it has disappeared as a breeding bird from much of this extensive area because of the drying up of its habitat. The trend of decline of the Mexican Duck and its breeding habitat, both in Mexico and the United States, indicates that it is probably in danger of extinction.

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PARASITISM BY THE BROWN-HEADED COWBIRD ON A BROWN THRASHER AND A CATBIRD

ROBERT M. MENGEL AND MARION ANNE JENKINSON

DESPITE the accumulation of an impressive body of information (summarized by Friedmann, 1929, 1963) on the breeding biology and social parasitism of the Brown-headed Cowbird (*Molothrus ater*), most of the evidence concerning the cowbird's activities at the nests of its hosts remains circumstantial, and reports of direct observations of these activities are remarkably few. Even in some of these instances it is difficult to interpret the evidence and one often wishes that more details had been given. In view of this, and following the example of Mayfield (1960:164-171), we herewith report our observations (all 1965) of parasitism by a cowbird on a Brown Thrasher (*Toxostoma rufum*) in some detail. Incidentally we have included some brief notes on a parasitized nest of a Catbird (*Dumetella carolinensis*).

OBSERVATIONS AT THE THRASHER NEST

4 May.—A pair of Brown Thrashers completed their nest. It was four feet up and well concealed at the east end of a dense climbing rose which extends 20 feet along the south side of a redwood board fence, just north of our home in Lawrence, Douglas County, Kansas.

5 and 6 May.—No observations.

7 May.—Very early in the morning we caught the female Brown Thrasher in our mist net. We do not know if she had been to the nest earlier that morning to lay an egg. She was badly entangled and we disentangled her with some difficulty. We banded and released her (USFWS 623-40000 and red color band). However, after she had flown some 15 feet, she dropped to the ground and we realized that she had probably sprained her wing. Because of this we watched her closely for the next several hours and were aware at all times of her location and condition. Through this period her mate closely attended her. Neither of the thrashers returned to the vicinity of the nest until late afternoon. At 11:00 we checked the nest. It contained one egg of the Brown Thrasher and one of a Brown-headed Cowbird.

At 12:32 a male and female cowbird flew in from the north and alighted on the fence, about 10 feet east of the thrasher nest and about 2 feet apart, the female being nearer the nest. After remaining thus for about two minutes, the female started edging towards the rose. She was followed by the male who precisely maintained their original distance of separation. The female's actions seemed entirely purposive—she seemed to know of the nest. She disappeared into the cover of the rose near the nest site. The male waited on the fence, facing north, just east of the rose. After about two minutes he flew off to the north. We did not see the female depart and thought she was still at the nest.

At about 12:40, a male and female cowbird appeared from the north and landed in a nearby tree. The male remained there, but the female flew to the fence top, just west of the rose, and immediately disappeared into the cover of the rose. In about 30

seconds, an empty-billed female cowbird emerged abruptly from the area of the nest, chattering sharply, and flew rapidly to the east. She was followed immediately by the male. Since we had seen "two" females arrive and only "one" leave, we assumed that one was still on the nest. Thus we waited eight minutes before investigating.

When we did, we found that no cowbird was at the nest and that the nest now contained only one egg—that of the thrasher. A short search revealed the fragmented shell of the still fresh cowbird egg, parts lying a few inches on either side of the fence, beneath the nest. The horizontal boards of this fence are so lapped that an egg could easily be dropped through one of the interstices. It seems highly probable that the "first" female had departed unseen through one of these openings, dropping the egg en route and being followed by the male. (This route later became the favorite one of the thrashers as they entered and left the nest area.)

8 May.—At 08:30 a female cowbird was seen perched about 10 feet west of the rose looking intently in the direction of the nest. The male thrasher was perched just west of the rose, erect and watchful; after a few minutes the cowbird flew away to the east. We immediately checked the nest, flushing the female which apparently had begun to incubate, and found another cowbird egg, but only one thrasher egg rather than the two we had expected. The female thrasher seemed to be fully recovered from her injury of the day before.

At 12:32 (almost exactly 24 hours after the visit of the day before) a female cowbird appeared alone on the fence a few feet west of the rose. Again, seeming quite purposive, she entered the cover and was out of sight just the requisite time to reach the nest. She then emerged with conspicuous abruptness and departed hastily eastwards, having discovered the female thrasher on the nest.

9 May.—Morning and evening checks of the nest revealed its contents unchanged. A thrasher flushed from the nest at 09:00, but the birds seemed somewhat less attentive than they had on 8 May, and none was on the nest at the evening check. At 18:48, a female cowbird appeared on the fence about 25 feet east of the rose. She took considerable time going to the rose but seemed entirely purposive. After a short time at the nest (as indicated by agitation of the surrounding vegetation) she departed to the north. The contents of the nest remained the same as before, i.e., one cowbird egg and one thrasher egg.

10 May.—At 10:00 the nest now contained two Brown Thrasher eggs and one cowbird egg.

11 and 12 May.—Situation unchanged. The thrashers seemed very attentive during these two days and one was flushed at the times of the three checks we could make (both mornings and the first evening).

13 May.—At 11:00 the nest was checked and a thrasher flushed. The nest contained two thrasher eggs but no cowbird egg. An immediate search revealed no trace of the missing cowbird egg, but we did discover an egg of a thrasher, one end embedded in the mud and its shell nearly intact save for the point of impact, where it was badly smashed. The yolk was hard and dry. It was just south of the fence, at a point previously unsearched, about six feet west of the nest and still within the confines of the rose.

Subsequent days.—The male thrasher evidently met with some accident and was not seen after 15 May. The female incubated her remaining two eggs in an increasingly desultory fashion for two more days, being last seen on 18 May. After that date two different thrashers appeared regularly in the yard. On 21 May we took the two abandoned thrasher eggs. They contained moderately advanced embryos.

OBSERVATIONS AT THE CATBIRD NEST

A pair of Catbirds built a nest in a forsythia bush about 25 feet from the site of the Brown Thrasher nest. Three Catbird eggs were laid in the nest, one each on 30 and 31 May, and 1 June, and two Brown-headed Cowbird eggs were laid there, one each on 31 May and 1 June. The female Catbird stayed at the nest much of the time after the appearance of her first egg, although we do not know if she was incubating. A female cowbird appeared near the bush on several occasions but she always disappeared behind the bush and we were not able to see if she went to the nest or flew directly away. In any event, no eggs were removed from this nest. The female Catbird was apparently incubating the cowbird eggs along with her own when the nest was destroyed by a violent hailstorm in the early evening of 1 June.

These data are presented because there are few records of a Catbird accepting cowbird eggs (see Friedmann, 1963:69-70). The fact that the cowbird did not remove any of the host's eggs from this nest may result from the very early attendance by the female Catbird to her nest.

DISCUSSION

Proprietary interest by cowbirds in nests of their hosts.—On the basis of his own observations of Kirtland's Warblers (*Dendroica kirtlandii*) and those of various other workers on other species, Mayfield (1961) concluded that cowbirds show a proprietary interest in nests which they have parasitized or are about to parasitize. Our observations strongly support that conclusion. In all, we recorded five visits to the thrasher nest by a female cowbird, ranging from 08:30 to 18:48 and on three days. Although we kept no record of our total observation hours, we spent a very small proportion of our time watching the nest, and the five visits thus suggest a high degree of interest by cowbirds in the nest site.

Pair bonds of cowbirds.—Our observations agree with those of Laskey (1950) which suggest that cowbirds form a pair bond and tend to occupy a certain area or "domain" (see pp. 166-167). Our two observations of a male cowbird accompanying a female to the nest site, and of his waiting for her while she went to the nest, seem to be unique. At no time did we see more than one male and one female in the area until 1 June, when a flock of 10 (about equal numbers of males and females) was seen in a neighbor's yard, about 100 feet from the nests in question. Throughout the period, a male cowbird frequently sang from a television antenna across the street. We are inclined to think, therefore, that we may have been observing the activities of only one pair of cowbirds, in their domain, and that all four eggs may have been those of one female.

Time of removal of eggs by a cowbird.—It now seems to be a well established fact that the female cowbird does not remove an egg at the time she lays, but does so any time from the day before to (rarely) the day after that event. Our observations support this fact although we were unable to

tell whether the cowbird was removing eggs in advance of or after deposition. The time of day of egg removal on 7 May was approximately 12:30. It is possible that the female which appeared at about that time on the next day also came for that purpose but was frustrated in her attempt by the presence of the female Brown Thrasher. This is somewhat later in the day than that observed by most, but not all, workers (see Norris, 1944, for a summary, and Mayfield, 1960:160).

Discrimination by the cowbird between eggs.—Our evidence clearly indicates that a cowbird egg was removed by a cowbird, on 7 May, and it seems very likely that the second cowbird egg was removed by a cowbird also.

We know of only a few other reported instances where the suggestion has been made that a cowbird had removed a cowbird egg from a host's nest. Mayfield (1960:164), in his extensive study, found no evidence that the cowbird ever made such a mistake at the nest of a Kirtland's Warbler. However, Hann (1937:204) found that approximately 30 Ovenbird (*Seiurus aurocapillus*) eggs and 4 cowbird eggs disappeared "under circumstances which indicated that the Cowbird had taken them." Laskey (1950:171–172) reported the apparent destruction by cowbirds of cowbird eggs in a nest of a Cardinal (*Richmondia cardinalis*) and one of the Rufous-sided Towhee (*Pipilo erythrophthalmus*). However, she found that at both nests several cowbirds had been engaged in heated disputes, and she concluded that the destruction of cowbird eggs resulted from the rivalry of two or more females.

Erwin E. Klaas (pers. comm.) has evidence (which he plans to publish later) which suggests that cowbirds have, on occasion, removed their own eggs from nests of the Eastern Phoebe (*Sayornis phoebe*). In these instances, however, the cowbird may have had no choice, since it is possible that only cowbird eggs were present.

It is possible that a cowbird also removed the cowbird egg which disappeared from one nest of a parasitized Brown Thrasher reported by Taylor and Goertz (1965).

Because the eggs of Kirtland's Warblers, Ovenbirds, and Brown-headed Cowbirds are all whitish and lightly speckled, Mayfield (1960:164, 1961:165) concluded that the cowbird discriminates on the basis of size. He noted (1961:165): "The mean size of Brown-headed Cowbird eggs in Kirtland's Warbler nests is 20.9 by 16.5 mm (N = 24); of Ovenbird eggs, 20.3 by 15.6 mm (N = 48, Hann, 1937:172); of Kirtland's Warbler eggs, 18.1 by 13.9 mm (N = 154)." We measured 27 Brown Thrasher eggs (which also are whitish and lightly speckled) in the University of Kansas collection, these being one each from 27 clutches taken in Johnson and Jackson counties in western Missouri. The eggs are highly variable in size, shape, and color, but they averaged 26.9 mm (range, 24.2–29.6) by 19.8 mm (18.9–21.2).

Thus, if the size of the egg is important, even in part, in the cowbird's ability to discriminate between eggs, we would expect a rather high percentage of mistakes to be made at Brown Thrasher nests, since in these the cowbird's egg is the smaller egg, the opposite of the situation with nearly all regular hosts. We think this might account for the fact that there are surprisingly few records of parasitism of Brown Thrashers (see Friedmann, 1963:71), the evidence regularly being destroyed by the cowbirds themselves.

SUMMARY

Two Brown-headed Cowbird eggs were laid in a Brown Thrasher nest. A male and female cowbird, which, from the attendance of the former on the latter, seemed likely to have a pair bond, twice visited the nest area. We think this was the female that also showed a high degree of interest in the nest on other occasions over several days. Both cowbird eggs were eventually removed from the nest, at least one being thrown out by a cowbird. The cowbird may discriminate between its own and, at least, similarly colored eggs on the basis of size and would thus be expected to make a high percentage of mistakes at Brown Thrasher nests.

Two cowbird eggs were also laid in a Catbird nest and were being incubated by the Catbird until the nest was destroyed by a storm.

ACKNOWLEDGMENT

We thank Erwin E. Klaas for sharing with us his data on cowbird parasitism of some Eastern Phoebe nests.

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MUSEUM OF NATURAL HISTORY, THE UNIVERSITY OF KANSAS, LAWRENCE, KANSAS,
29 MAY 1968.

HIGH DENSITY OF BIRDS BREEDING IN A MODIFIED DECIDUOUS FOREST

DAVID W. JOHNSTON

BREEDING bird populations in different mature upland deciduous forest communities commonly vary between 100 and 400 pairs per 100 acres (Kendeigh, 1961), although drastically altered habitats, such as those found in gardens and parks, might sustain as many as 1000 or even 1500 pairs per 100 acres (Pitelka, 1942; table 18.2 in Welty, 1963). For successful breeding in all these terrestrial habitats birds require sufficient food and feeding areas, nesting sites, singing perches, a general vegetational aspect, and perhaps other features. Changes in any of these biologic and physical features of the habitat will likely result in alteration of breeding success or population density or both. Turcek (1951), Oelke (1966), and others, for example, have noted that increased stratification of the vegetation in forests will generally result in higher breeding bird densities.

The present report considers a breeding bird population study at the University of Virginia Biological Station at Mountain Lake, Virginia between 19–29 June 1967. The Station, located atop Salt Pond Mountain at an elevation of 3800 feet, is surrounded by a second-growth oak-chestnut forest, although the chestnuts are now represented chiefly by sprouts due to blight. Dominant trees in the forest include white oak (*Quercus alba*), red oak (*Q. rubra*), cucumber tree (*Magnolia acuminata*), and black locust (*Robinia pseudo-acacia*). Mountain-laurel (*Kalmia latifolia*), blueberry (*Vaccinium corymbosum*), and flame azalea (*Azalea calendulacea*) are conspicuous shrubby plants. Beginning about 1930 the Station grounds have been partially cleared, and today present a park-like appearance (see photograph in Davis, 1959) because of the open lawns with their borders of preserved or planted mountain-laurel, *Rhododendron maximum*, blueberry, white (*Pinus strobus*) and pitch (*P. rigida*) pines, hemlock (*Tsuga canadensis*), and shrubby and herbaceous vegetation. An upperstory or canopy, although somewhat thinned out, consists of white, black, and red oaks, cucumber tree, and pines. The Station grounds differ, therefore, from the surrounding forests by having (1) open lawns, (2) an increase in the shrub layer, (3) thinned-out dominant trees, and (4) numerous (22) buildings that provided some additional nesting sites for Robins and Phoebes. One very small stream traverses a portion of the grounds. In a somewhat arbitrary fashion, we have divided the habitat into strata—ground layer, shrub layer, subcanopy, and canopy—a procedure similar to that of MacArthur and MacArthur (1961) in their use of “foliage height profiles.” Also, we have adopted the

stratal limits suggested by Elton and Miller (1954): ground layer, 0–½ ft; shrub layer, ½–6 ft; subcanopy, 6–15 ft; canopy, > 15 ft. The only difficulty with these limits in our study lies with the canopy which has a vertical range of 15–60 ft.

The breeding bird census was conducted by the author and 10 students on 10 acres that included most of the Station grounds described above. A territory-mapping technique was utilized: territorial limits of all birds on the area were accurately mapped as were occupied nests. Individuals or pairs whose territories were at the edge of and not within the 10-acre plot have been excluded from our totals. Furthermore, at least 7 additional species (potential breeders) were classified as visitors to the area because they were observed too infrequently to be considered as part of the current breeding population.

The results of our census at the Station (Table 1) showed 80 pairs (including some apparently unmated males) and 22 species on 10 acres (= 800 pairs per 100 acres). These figures differ markedly from those of Chandler (1960) for birds breeding in the deciduous forest neighboring the Station grounds. He found only 16 species and 190 pairs per 100 acres. Of the 22 species occupying territories on the Station grounds in 1967, 11 also bred in the contiguous second-growth hardwood forest and 6 in a forest-edge habitat. The three species with the highest breeding densities at the Station (Robin, Cedar Waxwing, Least Flycatcher), however, were absent in the nearby forests in 1967; neither were they represented in the hardwood forest communities studied by Chandler. The most abundant birds reported by Chandler were Ovenbird (*Seiurus aurocapillus*), Rose-breasted Grosbeak, and Red-eyed Vireo: of these three, only the Ovenbird had a higher breeding density in the nearby forests than on the Station grounds. At this elevation in the Virginia mountains and considering the generally continuous, unbroken stretches of deciduous forest, it is virtually axiomatic that forest-edge species, such as Indigo Bunting, Slate-colored Junco, Brown Thrasher, and Rufous-sided Towhee, would be restricted to and most abundant at the edge of small clearings or associated with roadside vegetation. The Station grounds obviously provided the edge-effects required by these species.

The high density of breeding birds at the Station appears to be attributable to two principal factors. First, as compared with vegetational aspects found in neighboring forests, artificial plantings of rhododendron and hemlock at the Station increased the shrub layer, thus increasing an edge-effect and more nesting sites for certain species. Second, and probably of greater significance than nesting site alone, is the fact that a partial clearing of the forest increased the distance between trees and introduced open spaces both horizontally and vertically, thereby effectively increasing feeding areas for

TABLE 1
BREEDING BIRDS ON 10 ACRES OF MODIFIED DECIDUOUS FOREST
AT MOUNTAIN LAKE, VIRGINIA IN JUNE 1967.

Species	Stratum ¹ and mean nest height in feet	Number of occupied nests	Number of additional pairs	Number of additional territorial males	Totals
Robin (<i>Turdus migratorius</i>)	C-SC; 23	14	2	1	17
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	C-SC; 28	10			10
Least Flycatcher (<i>Empidonax minimus</i>)	C-SC; 28	7			7
Catbird (<i>Dumetella carolinensis</i>)	SC-S; 9	6			6
Chipping Sparrow (<i>Spizella passerina</i>)	C-SC; 31	4	1	1	6
Slate-colored Junco (<i>Junco hyemalis</i>)	G	3	1	1	5
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	G	2	1		3
Rose-breasted Grosbeak (<i>Phenicicus ludovicianus</i>)	C-SC; 36	3			3
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	SC ; 8	2	1		3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	SC-C; 13	4			4
Scarlet Tanager (<i>Piranga olivacea</i>)	C ; 40	2			2
Indigo Bunting (<i>Passerina cyanea</i>)				2	2
Solitary Vireo (<i>Vireo solitarius</i>)				2	2
Eastern Phoebe (<i>Sayornis phoebe</i>)		2			2
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	C		1		1
Tufted Titmouse (<i>Parus bicolor</i>)	C		1		1
Brown Thrasher (<i>Toxostoma rufum</i>)	G	1			1
Wood Thrush (<i>Hylocichla mustelina</i>)	C ; 20	1			1
Blackburnian Warbler (<i>Dendroica fusca</i>)	C			1	1
Flicker (<i>Colaptes auratus</i>)	C ; 40	1			1
Crested Flycatcher (<i>Myiarchus crinitus</i>)	C		1		1
Wood Pewee (<i>Contopus virens</i>)	C ; 40	1			1
Totals		63	9	8	80

¹ C—ground; S—shrub, SC—subcanopy, C—canopy;
See text for limits of strata.

many species (Robins, flycatchers, ground-nesting species). The Station grounds, therefore, comprised a kind of forest and forest-edge "oasis" wherein vegetational strata, poorly represented, absent, or unmodified in the contiguous forests, could support an exceptionally high population of breeding birds.

Appreciation is given here for facilities and courtesies provided by the University of Virginia Biological Station.

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- DEPARTMENT OF ZOOLOGY, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA,
8 APRIL 1968

ANNOUNCEMENT

The 1970 Annual Meeting of the Western Bird Banding Association will be held at the Point Loma Inn, San Diego, California, on 24-26 April. Paper sessions and workshop discussions of new techniques and banding problems will be held on Saturday. On Sunday there will be several field trips including a boat trip to see pelagic species. For more complete information write to Dr. Charles T. Collins, Dept. of Biology, Calif. State College, Long Beach, Calif. 90801.

INDEXING POPULATION DENSITIES OF THE CARDINAL WITH TAPE-RECORDED SONG

DOUGLAS D. DOW

IN studying habitat utilization by the Cardinal (*Richmondia cardinalis*), I required information about the relative densities of populations in different regions. As indexing population densities was not a primary objective, I sought a rapid method that would yield consistent and comparable results.

Many standard techniques of measuring population density (e.g., Kendeigh, 1944) were impracticable in my large study areas (15 by 15 miles). Roadside counts (Kendeigh, 1944; Howell, 1951; Hewitt, 1963) did not appear promising as Cardinals are seldom seen along roadways in southern Ontario where I began this work. Since the Cardinal is a loud singer and is netted easily using a recorded song and a mounted bird as a lure, I developed a modified roadside count method utilizing responses to tape-recorded song.

Listening counts along roadways are well known to workers in gamebird management (Kimball, 1949; Rosene, 1957; Foote, et al., 1958; Smith and Gallizioli, 1965; Gates, 1966). Tape-recordings have been used to locate birds (Bohl, 1956; Levy, et al., 1966). In census methods, Stirling and Bendell (1966) used tape-recorded female calls to stimulate calling of the Blue Grouse (*Dendragapus obscurus*), and Giltz (1967) used recorded alarm cries of young Red-winged Blackbirds (*Agelaius phoeniceus*) to stimulate flight of adults.

BASIC TECHNIQUE

An automobile is driven to a predetermined point on a road, and three amplified tape-recorded Cardinal songs are played in 15 seconds. An observation period of 30 seconds follows when the number of responding birds are counted. The procedure is conducted four times, bringing the total observation time to two minutes. A "response" is defined as the singing of a Cardinal or the approach of a non-singing male. About 20 points could be sampled in two to three hours if the points were selected at random from a grid of one-mile cells, represented about 60 per cent of the total study area, and were sampled via the shortest connecting route. In other applications when sample points were non-random, e.g., a line transect with points one mile apart, sampling was somewhat faster, and about 10 points could be sampled per hour. The index value is the average number of Cardinals responding at the sampled points.

Songs were broadcast from a continuous loop of tape and fed through a 12 watt transistorized amplifier and a 7.5 watt loud speaker fitted with a horizontal, circular baffle and mounted vertically on a car window. The baffle and vertical mounting were

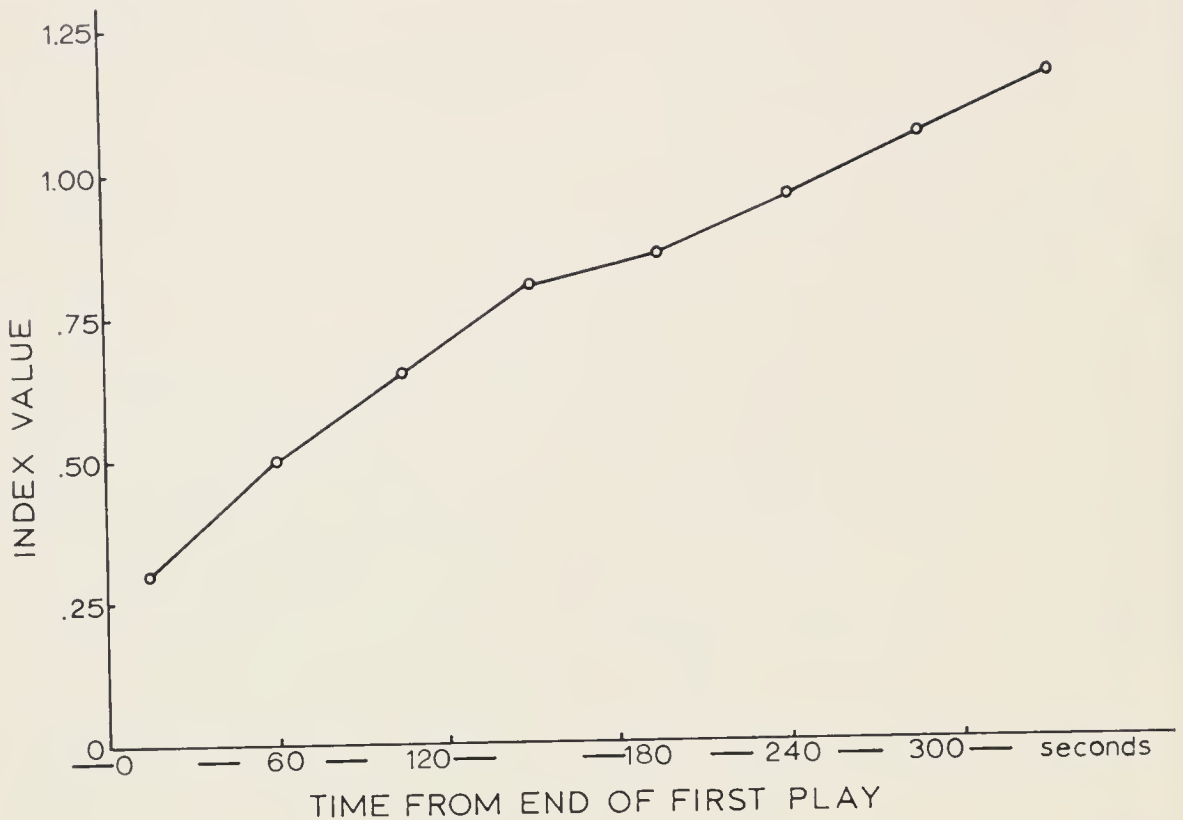


FIG. 1. Cumulative increase in index value with extended observation periods. Plotted points represent the average of 20 points sampled shortly after sunrise on 27 and 28 March 1966 near Lambeth, Ontario. Solid lines on time scale indicate playing of tape-recorded song.

used to distribute the sound as uniformly as possible. A meter, connected across the voice coil, monitored the output level of the signal. The volume level used was empirically determined as that which a listener could just hear at one-quarter mile, approximately the average maximum distance that a singing Cardinal can be heard.

Urban areas and heavily travelled paved roads were avoided because of the noise usually associated with them.

INCREASE IN RESPONSE OVER NORMAL SINGING

Figure 1 shows the effect of continuing observation periods beyond the four normally used. The cumulative increase in index value shows almost no levelling off even by the eighth period. My selection of four observation periods is, therefore, arbitrary and results in a conservative index value; it is a compromise between a large number of observation periods and the maximum number of points that can be sampled in a reasonably short time.

There is no doubt that the use of tape-recordings increases the number of birds heard or seen (Table 1). The difference in percentage increase between April and July is typical; the spontaneous singing of the species is decreasing throughout this period while the responses to recordings remain about the same.

TABLE 1

INCREASE IN RESPONSE ATTRIBUTABLE TO THE USE OF TAPE-RECORDINGS†

Locality (Nearest town)	Sampling dates	Index value		Percentage increase	No. of points sampled	P*
		Without tape	With tape			
Lambeth, Ontario	18-19 April	0.600	1.000	67	20	NS
Melbourne, Ontario	21-22 July	0.290	0.613	111	31	< 0.025
Melbourne, Ontario	15-16 July**	0.161	0.419	160	31	< 0.01
Dresden, Tennessee	22-23 June	2.95	4.05	37	20	< 0.005

† In all additional comparisons, the number of Cardinals responding to tape-recordings was always greater than the number noted without recordings.

* Significance level of one-tailed Wilcoxon Signed Rank Test of difference between dependent means (Siegel, 1956).

** Sampled between 10:30 and 13:30 hours. All others were sampled just after sunrise.

FACTORS INFLUENCING RESPONSE

It is important to standardize as many conditions as possible in a technique such as this. The method is not only susceptible to vagaries of weather, as are most field experiments, but to almost any distracting sound, particularly traffic and tractor noise.

The acoustic influence of topography and cover on both broadcast songs and responses presents too formidable a complex of factors for investigation here. It is assumed that such factors cancel each other over a large area. Also, they are largely mitigated in successive comparisons of the same areas.

The only main climatic factors that appear to appreciably influence responses are wind and rain. As wind increases, the observed responses decrease. Light to moderate rain seems to inhibit singing, and the drumming of rain on roads and nearby vegetation makes listening impossible. There was no evidence that even very dense fog had any influence on responses, although spontaneous singing seemed somewhat suppressed.

The distribution of responses obtained at different times of day is shown in Figure 2. The response drops from a morning peak to a low level in mid-afternoon, then rises again in the evening, but not to the same high level as morning song. This is somewhat similar to the diurnal pattern of spontaneous singing of many passerine birds (Van Tyne and Berger, 1959:147). Subsequent sampling indicated that the ratio between means of morning and evening samples was not constant enough for reliable estimation of morning

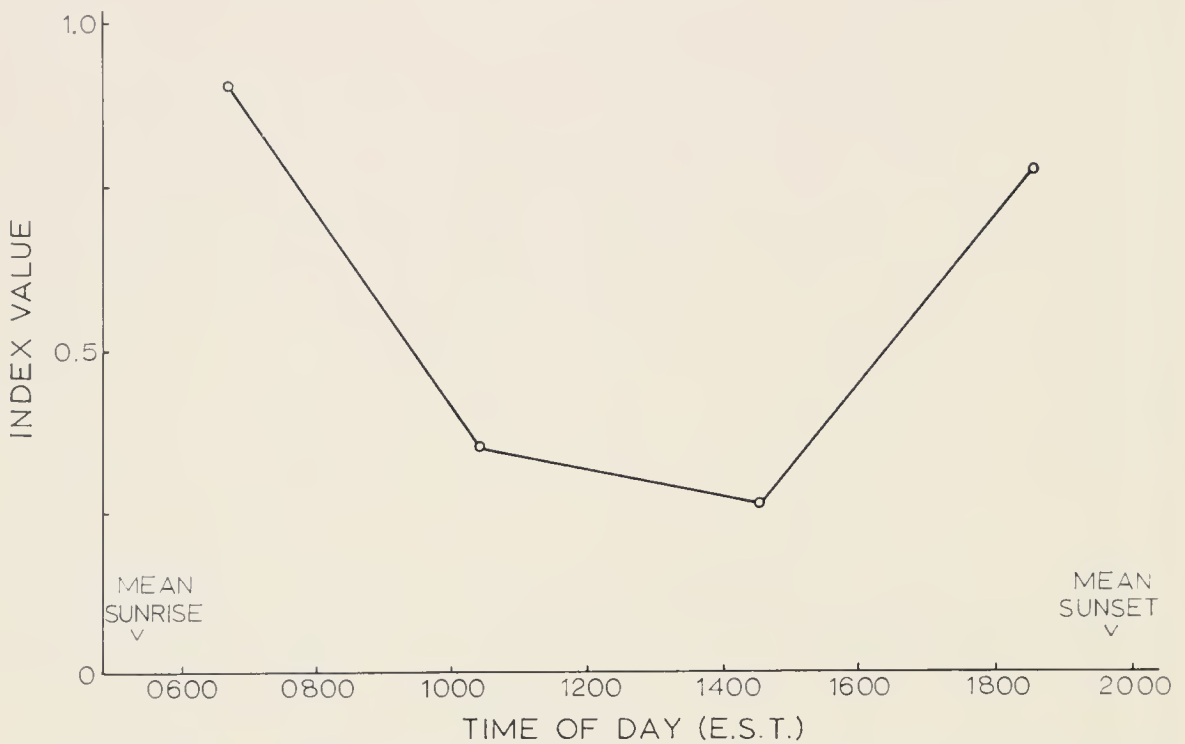


FIG. 2. Distribution of responses obtained from sampling the same 84 points at four different times of day near Melbourne, Ontario, between 2 and 13 August 1964. ($P < 0.01$ in Friedman two-way analysis of variance.)

values from adjusted evening values. This inconstancy was probably attributable to the greater chance of wind in the evening and also to an increase in human activities in some areas. Thus, all further sampling was restricted to morning hours; each sample route was begun between the onset of civil twilight and sunrise, which is about the time that this species normally begins to sing (Allard, 1930; Leopold and Eynon, 1961; Wiens, 1960).

Davis (1965) has pointed out that more singing birds may be noted at the beginning of a census period than at the end. I have found the same to be true using tape-recordings, predictable, of course, from Figure 2. But by repeating several sample routes in reverse order at the same time on different days, I discovered that although more birds are counted in the early half of sampling, the average number remains constant.

Abrupt changes in response occur in early spring at the onset of seasonal singing and again late in the summer when reproductive activity wanes. However, during the intervening period, responses remain fairly constant (Fig. 3) while spontaneous singing steadily declines. Herein lies one of the principal advantages of using tape-recordings to stimulate song since the method is not restricted to the spring when birds are most active. In Ontario, consistent results were obtained between late February and mid-August. In Tennessee, a sudden decline of spontaneous singing and con-

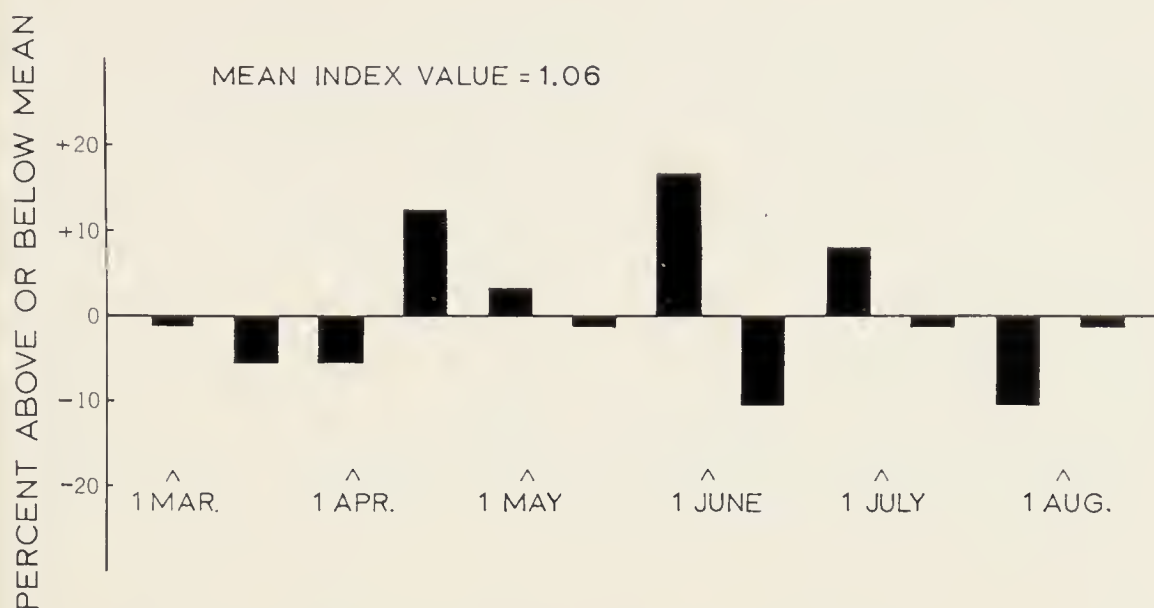


FIG. 3. Variability of index among 12 samples of the same 20 points near Lambeth, Ontario, in 1965. Points were sampled approximately every 14 days.

current reduction of response to tape-recorded song occurred in late June. However, as spontaneous singing begins somewhat earlier in the season, it is likely that the technique would also be applicable early in the year.

I did not experiment with the volume of playback song, but used a standard level previously described. The Cardinal, in Ontario, has a repertoire of some 10 to 19 song types (Lemon, 1966). I used a song that is widespread throughout the species' range; it corresponded approximately to type WBW of Lemon's classification.

A bird's reaction to a foreign conspecific song may be quite different from that to a neighbor's song (Frings, et al., 1958; Weeden and Falls, 1959). Slightly fewer Ontario birds, at the same set of 20 points, responded to songs recorded 17 miles to the west and 37 miles to the east (mean values of 0.85 versus 1.15 and 0.90 vs 1.15 respectively); whereas, slightly more Tennessee birds responded to an Ontario song recorded 627 miles NNE (Ontario, 3.65; Tennessee, 3.52). A reciprocal test in Ontario showed similar results (Ontario, 1.22; Tennessee, 1.32). This suggests that there may be slight differential response associated with different populations. However, as none of these differences are statistically significant, they appear negligible for this application. Lemon (1967) has shown different numbers of songs by Cardinals responding to different dialects, but his work shows no appreciable difference in numbers of birds responding.

Perhaps the greatest disadvantage of this, and of any technique involving listening, is its limited applicability in regions of high population density. Where large numbers of birds can be expected to respond at a point, I think

TABLE 2
COMPARISON OF RESULTS OBTAINED IN FOUR STUDY AREAS[†]

	Ontario			Tennessee
	Melbourne	Simcoe	Elmira	Dresden
Area (square miles)	625	625	225	225
No. of points sampled	160	160	140	140
Total birds responding	155	60	31	598
Index value*	0.97	0.38	0.22	4.3
Range of birds per point	0-4	0-2	0-2	1-8

[†] Areas were sampled in late April and early May from 1965 to 1967.

* A significant difference ($P < 0.001$) was found among these values using the Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

that close singers tend to mask more distant ones, resulting in too few birds being scored. I believe that the low increase in Tennessee (Table 1) resulted because not all birds responding to the tape were actually counted: whereas, the fewer birds singing spontaneously had a higher probability of being noted. The bias introduced by singing females is considered to be negligible as I found during sampling that fewer than one per cent of singing Cardinals of known sex were female.

A further consideration should be kept in mind by anyone using this or any technique involving tape-recording. A recorded song or call, unless played at a volume well below the normal singing level of the species, can never be regarded as a *constant* stimulus. Birds responding to a recording probably increase the stimulus value for other conspecifics within hearing range. Consequently, in a dense population, which may only be a very local condition, a recording may have a higher effective stimulus value than in a sparse population if few birds are singing prior to the broadcast; the opposite may be true if most birds are already singing.

APPLICATIONS OF THE TECHNIQUE

The technique has proved useful in providing a relative index of abundance of the Cardinal in large study areas in different parts of its range. The recording used was obtained locally for each study area. The results are shown in Table 2. The area in Ontario with the lowest index value was selected because of its location on the periphery of the Cardinal's range; the Tennessee area was selected as probably being representative of the center of the range. A significant difference ($P < 0.001$) was found among the four indices.

Temporal changes in density can be detected similarly. I checked 20 points near Lambeth, Ontario, twice in 1965 (22 April and 31 July) and 1966 (22

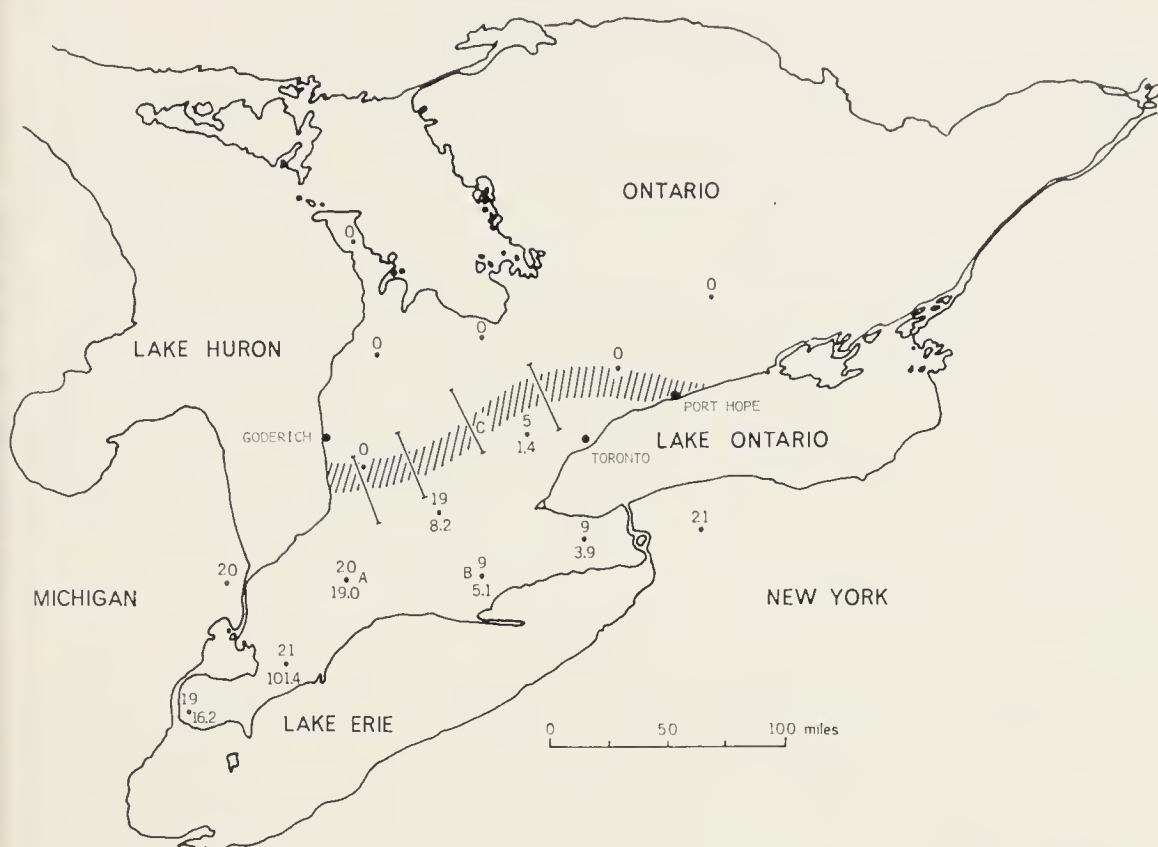


FIG. 4. Each solid circle shows the center of an area of 20 points sampled in July 1965. The total number of birds responding at these points is shown above the location. Below the location is the number of birds per 100 hectares of woody cover, where cover was measured from aerial photographs in a circle of one-quarter mile radius about each sample point. Letters A, B, and C show the approximate center of the study areas of Table 2, i.e., Melbourne, Simcoe, and Elmira respectively. The cross-hatched zone shows the edge of the Cardinal's range based on four 30-mile transects (straight lines) sampled in August 1966 in addition to the figures shown. A few small, extralimital populations are known to the north and east of this area.

March and 5 August). The two sets were averaged for each year, yielding indices of 1.02 and 1.40 respectively. The significant difference ($P < 0.05$ in Wilcoxon Signed Rank Test) suggested an increase in the population of the area.

The technique has proved very useful for obtaining information on distribution (Fig. 4). A gradient of density can be seen across southern Ontario from west to east. The difference in the index value of New York state and the adjacent regions of Ontario may result from the heavily industrialized urban area along the Niagara River acting as a barrier or buffer to the recent build-up in population density in New York described by Beddall (1963). I found the edge of the range to be fairly abrupt, and not apparently correlated with type of vegetation.

RELATION OF INDEX TO POPULATION DENSITY

This technique was developed to yield a relative index, not an absolute measure of density. Because of the masking effect previously suggested in very high densities, the relationship between the index value and the real density is likely linear only in low densities. The measurement scale of the index is undoubtedly at least ordinal, i.e., an increase in index value under similar environmental conditions indicates an increase of unspecified magnitude in population density. Independent estimates of density in two of my study areas using the method of Hayne (1949) yielded 0.74 males per ha (30 per 100 acres) of undifferentiated habitat in Tennessee and 0.012 per ha (0.48 per 100 acres) in Ontario (Elmira). Of course, many more areas of different density would require sampling by the two methods to establish a continuous relationship.

SUMMARY

A roadside technique was developed for indexing population densities of the Cardinal by counting birds after the playing of a tape-recorded song. The mean number of birds responding at sample points was used as an arbitrary index. The use of tape-recordings resulted in a marked increase of birds seen and heard. Numbers of responding birds were influenced by rain, wind, and time of day. Seasonal fluctuation was relatively small, permitting the technique to be used into late summer. The method has been used to obtain indices of relative abundance in different parts of the Cardinal's range, to compare the same area for annual differences, and to delimit the range in southern Ontario. The relationship between index and actual density is virtually unknown, but is probably close to linear in low densities. Hence, the technique is better suited to moderate population densities than to very high ones. Where a rapid method of detecting differences in densities is required, the technique should work well for any species having a loud or distinctive song or call.

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GENERAL NOTES

On the validity of some supposed "first state records" from Yucatán.—In a paper presenting miscellaneous "noteworthy records of birds from the Republic of Mexico," Thompson (Wilson Bull., 74: 173–176, 1962) included a number of specimens collected by George F. Gaumer, now in the University of Kansas Museum of Natural History. These were listed with no qualifying remarks whatsoever, mostly prefaced by the asterisk used by Thompson to indicate "first occurrences in Mexican states."

Thompson may not have been aware that the data on Gaumer specimens are notoriously unreliable. Gaumer was a physician who resided in Yucatán during the late nineteenth and early twentieth centuries. Although a tireless collector, he was careless and inconsistent about labeling his specimens. Many were apparently labeled from memory months and even years after collecting (Paynter, Peabody Mus. Nat. Hist. Bull., 9: 79 [and elsewhere], 1955). Many of Gaumer's specimens labeled "Cozumel Island" represent mainland species not otherwise known from the island, and it is now the custom among students of Mexican birds to disregard records from Cozumel and other islands in the Yucatán region that are based *solely* on Gaumer specimens (Paynter, *op. cit.*; Bond, 6th Suppl. Check-list Bds. West Indies (1956): 4–5, 1961; Parkes and Phillips, Condor, 69: 78, 1967).

Like most Gaumer specimens, those at the University of Kansas bear only the Museum's labels. This is not necessarily an indication that an original Gaumer label has been removed. Gaumer was apparently in the habit of sending off boxes of *unlabeled* specimens to various museums, where "Yucatan" labels would be attached. Most of the Kansas specimens are simply labeled "Yucatan," and Thompson has taken this to mean the *state* of Yucatán, which occupies only the northernmost third of the Yucatán Peninsula. In Gaumer's day the name "Yucatán" encompassed the entire area now divided among the states of Yucatán and Campeche and the territory of Quintana Roo. There is no justification for assuming that old "Yucatán" specimens necessarily constitute records for the area included in the modern state of that name.

Individual records in Thompson's paper based on Gaumer specimens are discussed below.

Sharp-shinned Hawk (*Accipiter striatus velox*).—Two specimens labeled Cozumel Island, considered by Thompson to be the first record from Quintana Roo. This species is apparently a rare migrant in the Yucatán area (Paynter, *op. cit.*: 58) and in the West Indies (Bond, *Birds of the West Indies*, 56, 1960), so a record from Cozumel is at least plausible. The species should not, however, be added to the Cozumel and Quintana Roo lists on the sole basis of these Gaumer specimens.

Lineated Woodpecker (*Dryocopus lineatus similis*).—Two specimens alleged to have been collected on Cozumel Island. This is a most implausible record. No other visitor to the island has reported this large, noisy, conspicuous woodpecker. During three collecting trips to Cozumel, neither I nor any of my field companions (A. R. Phillips, R. W. Dickerman, Juan Nava S.) saw either this species or any evidence of the diggings of a woodpecker any larger than the resident *Centurus*. The Lineated Woodpecker should be added to the list of "land birds apart from what are certainly North American migrants" that are known from Cozumel only from dubious Gaumer specimens, as published by Bond (*Caribbean J. Sci.*, 1: 41–42, 1961).

Fork-tailed Flycatcher (*Muscivora tyrannus*).—One specimen listed as the "first record" from the state of Yucatán. The species has been reported from Campeche and Quintana Roo; although its occasional occurrence in what is now the state of Yucatán

would not be unlikely, it should not be so recorded on the basis of a Gaumer "Yucatan" specimen.

Western Kingbird (*Tyrannus verticalis*).—One specimen from "Yucatan." This species has not been reported from any locality in the Yucatán Peninsula, or, for that matter, anywhere in Caribbean México south of San Luis Potosí. This specimen is not an acceptable basis for the inclusion of the Western Kingbird in the list of birds of the Peninsula.

Common Tody-Flycatcher (*Todirostrum cinereum finitimum*).—This "Yucatan" specimen may or may not be authentic, but is of no importance. Paynter (op. cit.: 201) recorded the species from Campeche and Quintana Roo. Dale A. Zimmerman saw a singing male at Sisal, Yucatán on 9 May 1956. This is the earliest authentic record known to me from the state of Yucatán, but numerous individuals have been seen and several collected since that time. William H. Buskirk of Louisiana State University estimated at 48 the number of Tody-Flycatchers in a narrow strip of coastal scrub, some 2½ km long, near Progreso on 21 August 1967.

Violet-green Swallow (*Tachycineta thalassina lepida*).—There is no other report of this species from anywhere in the Yucatán Peninsula, or, to the best of my knowledge, anywhere in the Caribbean lowlands of México. It is therefore a temptation to dismiss this record out of hand. However, the specimen is the *only* mainland one among the Gaumer specimens listed by Thompson that bears any data more precise than simply "Yucatan." According to the label, the bird was taken in 1914 at the "Port of Silam" [= Dzilam Puerto]. Even with a specified locality and year, however, some doubt must linger about the authenticity of a unique Gaumer record such as this one. I would recommend that the Violet-green Swallow be placed on the hypothetical list for the Yucatán Peninsula.

Orange-crowned Warbler (*Vermivora celata orestera*).—There is no other published record of this species from the Yucatán Peninsula, and the very fact that the one Gaumer "Yucatan" specimen represents the Rocky Mountain subspecies would ordinarily be enough to discredit the record. However, on 8 November 1963, an Orange-crowned Warbler was netted in the coastal scrub near Progreso by Phillips, Dickerman, and the writer. To our surprise, this bird was, indeed, referable to *orestera*. A second specimen, netted in the same area on 23 January 1965, is also nearest *orestera*, although approaching *celata* in the color of the interscapular area (A. R. Phillips, in litt.). It is possible, therefore, that Gaumer's specimen is authentic, but it is fortunate that examples with full data exist to substantiate the occurrence of this western form in Yucatán.

Nashville Warbler (*Vermivora ruficapilla ruficapilla*).—One specimen from "Yucatan." Paynter (op. cit.) did not list this species at all from the Peninsula, but Miller et al. (Pacific Coast Avifauna 33: 240, 1957) record the nominate race from Campeche without further details. It is conceivable that the species might reach Yucatán, but the one Gaumer specimen should not be used as the basis for a definite statement.

Northern Waterthrush (*Seiurus noveboracensis "noveboracensis"*).—This species is a common and well-known migrant and winter visitor throughout the Yucatán Peninsula and adjacent islands. Thompson lists one "Yucatan" specimen identified as the "first record" for the state of Yucatán of the nominate race, which Paynter (op. cit.: 254) reported only from Banco Chinchorro and Cozumel Island, Quintana Roo. Paynter referred all of his own mainland and island specimens (as well as, tentatively, his sight records from additional islands) to *S. n. notabilis*. However, I agree fully with Eaton (Auk, 74: 229-239, 1957) that the variations in color and size exhibited by this species cannot be utilized in any meaningful definition of geographic races. Having

seen for myself the series of breeding birds upon which Eaton's conclusions were based, I must reject Monroe's rather tentative demurrer (Amer. Ornithol. Union Monogr., 7: 335-336, 1968) to the effect that "three races seem to be recognizable." Monroe did not admit "*uliginosus*" of Newfoundland, which, as Eaton pointed out, represents clinal extremes in both color and size, and is one of the few discrete populations that approach definability. Specimens I collected on 4 and 18 November 1965 on Cozumel Island represent virtually the extremes in whiteness and yellowness of underparts within this species, but I attach no taxonomic significance to this, and use the binomial for all Northern Waterthrushes.

Wilson's Warbler (*Wilsonia pusilla pileolata*).—This species is such an abundant migrant and winter visitor throughout most of México that its apparent total absence from the Yucatán Peninsula has been all the more conspicuous. In the face of the lack of any authentic specimens, the fact that no less than four Gaumer specimens bear "Yucatan" labels would be enough to suggest the improbability of their supposed origin. Nevertheless, it is likely that the Wilson's Warbler is at least a rare transient in the Yucatán Peninsula. Specimens have been collected in British Honduras, at the southeastern base of the Peninsula (Russell, Amer. Ornithol. Union Monogr., 1: 159-160, 1964). I have received from William H. Buskirk a convincing account of sight records of single birds seen 13 and 14 September 1967 at Puerto de San Felipe, near Río Lagartos, Yucatán. The Gaumer specimens are referable to *W. p. pileolata*, whereas Russell (loc. cit.) identified British Honduras specimens as *W. p. pusilla*. Mr. Buskirk's sight record is, of course, unidentifiable subspecifically. I believe the *species* can safely be admitted to the list of birds of the Yucatán Peninsula, but the true status of the subspecies occurring there must await collection of specimens of more certain origin than those of Gaumer.

Baltimore Oriole (*Icterus galbula*).—This species has been recorded from Campeche and Quintana Roo, and could conceivably occur on migration within what is now the state of Yucatán, but the single Gaumer "Yucatan" specimen cannot substantiate such occurrence.

Montezuma Oropendola (*Gymnostinops montezuma*).—The attribution of this large rain forest species to the arid state of Yucatán on the basis of a Gaumer "Yucatan" specimen is perhaps the most implausible of Thompson's "first records." This oropendola is known from suitable habitat in Campeche and Quintana Roo, in the southern part of the Peninsula.

Western Tanager (*Piranga ludoviciana*).—There are authentic records of this western species on the Caribbean slope of México, but none from the Yucatán Peninsula. The pair of birds in the Gaumer collection should not form the basis for a statement of occurrence of this species either in the Peninsula or in the state of Yucatán.

Black-headed Grosbeak (*Pheucticus melanocephalus melanocephalus*).—The pair in the Gaumer collection, if authentic, would represent not only the first record for the state and peninsula of Yucatán, but the entire Caribbean lowlands of México as well. The Gaumer specimens do not provide adequate proof of such occurrence.

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I am indebted to Dale A. Zimmerman and William H. Buskirk for permission to utilize data from their unpublished field notes, and to Allan R. Phillips and Robert W. Dickerman for reading the manuscript as well as for companionship in the field in México. Dr. Phillips also supplied some essential points of information on distribution. For the privilege of examining some of the Gaumer specimens in the University of Kansas Museum of Natural History, I am indebted to Richard F. Johnston and Robert M.

Mengel. My field work in Mexico was supported by the Edward O'Neil Fund of Carnegie Museum and the Frank M. Chapman Memorial Fund of the American Museum of Natural History. Permits to collect birds in México were obtained through the kindness of Rodolfo Hernández Corzo of the Departamento de Conservación de la Fauna Silvestre.—KENNETH C. PARKES, *Carnegie Museum, Pittsburgh, Pennsylvania, 5 December 1968.*

High density Mallard nesting on a South Dakota island.—In May 1967, commercial fishermen reported large numbers of Mallards (*Anas platyrhynchos*) nesting on a 19-acre island located in the southeastern portion of 4,360-acre Lake Albert in Kingsbury and Hamlin Counties, eastern South Dakota. We visited the island on 18 and 27 May 1967 and confirmed the presence of numerous nesting Mallard hens.

Lake Albert is a large, open-water lake which supports fish populations. Emergent aquatic vegetation is scarce, and is confined to a few protected shore areas. The island lies about 450 yards northwest of the southeast shore of the lake. On the western half of the island is a 9-acre flat, while the eastern half contains a slightly sloping open area of about 2 acres surrounded by trees and shrubs. The 9-acre flat was dominated by a dense growth of tall nettles (*Urtica procera*) about 6 to 18 inches high during May. Patches of figwort (*Scrophularia* sp.), snowberry (*Synphoricarpos occidentalis*), wild black current (*Ribes americanum*), Missouri gooseberry (*R. missourienses*), chokecherry (*Prunus virginiana*), and rose (*Rosa* sp.), also grow on the 9-acre flat and other portions of the island. Indian hemp (*Apocynum sibiricum*), common milkweed (*Asclepias syriaca*), and sunflower (*Helianthus annuus*) are also found in open areas, while bluegrass (*Poa* sp.) was common in the more wooded eastern portion of the island. The entire island is ringed by trees, including box-elder (*Acer negundo*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), green ash (*Fraxinus pennsylvanica*), and willow (*Salix* sp.).

In 1967 and 1968 we searched approximately 50 per cent of the 9-acre flat after preliminary investigation disclosed that nearly all nests were confined to this area. In 1967, 39 Mallard nests were found, including 36 active and 3 abandoned. In addition, three hens were flushed from cover and their nests were not located. The same area was searched on 27 May 1968; 28 active nests were found, two hens were flushed from cover and their nests were not located. Of 67 nests observed during the two years, placement in various cover types was as follows: tall nettle, 91 per cent; gooseberry, 5 per cent; snowberry, 3 per cent; and bluegrass, 1 per cent. Based upon our sample of about 50 per cent of the preferred nesting cover, we estimated that there was a minimum of 78 and 60 nests in 1967 and 1968, respectively on the island.

Within the area sampled in 1967, the average distance between nests was 34 feet (range 7–150 feet). Measurements were not made in 1968. Clutch sizes averaged 10.4 eggs in 1967 and 8.8 eggs in 1968. Clutch sizes ranged from 6 eggs to 18 during both years with larger clutches more common in 1967 when a higher nest density was found. In 1967, six clutches contained 14 or more eggs while only one clutch contained 14 or more eggs in 1968.

No evidence of activity by egg predators was observed during the two years, except for the occurrence of a large garter snake (*Thamnophis* sp.) in 1967. Of 67 nests observed, none had been destroyed by predators although three nests had been abandoned. A Great Horned Owl (*Bubo virginianus*) nest containing two young was on the island in 1967; however, there was no evidence that the owls had been preying on Mallards.

During our visits to the island, pairs were continually observed moving between the

island and wetlands on the adjacent mainland. Numerous aerial pursuit flights were observed, but these intraspecific conflicts did not prevent the establishment of a high nest density, nor interfere with an apparently high hatching success. Lone and grouped drakes utilized waiting sites on waters surrounding the island while hens were laying or incubating. Several males were observed waiting for hens on land in close proximity to nests. On 27 May 1967 about 30 drakes were observed loafing together on an exposed, elevated site in the 9-acre flat. Many of the nesting hens in surrounding cover were in mid to late stages of incubation during this period.

The wind-swept, open water lake surrounding the island provided poor brood rearing habitat. Apparently, most hens moved their broods about 450 yards to the southeast shore where a large permanent marsh was located. We observed several newly hatched Mallard broods on this marsh on 27 May 1967.

Other ground nests found on the 9-acre flat included Mourning Doves (*Zenaidura macroura*), and one Ring-necked Pheasant (*Phasianus colchicus*). One Mourning Dove ground nest in nettles was located within 3 feet of an active Mallard nest.

The island was purchased by the South Dakota Department of Game, Fish and Parks in February 1944. During the mid-1950's adjacent landowners complained of the noxious weeds on the island, since they felt it to be a seed source that contaminated their fields. Consequently, the Department sprayed and cultivated the 9-acre flat for two consecutive years. This disturbance may have been responsible for increases in nettles since the mid-1950's.

This extremely high nest density contrasts with the usual widely-dispersed nest placement of Mallards in other portions of the prairie pothole habitat in North America. Such a concentration of nesting Mallards is probably a result of high nesting success and a high rate of migrational homing of both adult and first-year nesting hens. This high island nesting density of Mallards is similar to that described by Duebbert (Wilson Bull., 78:12-25, 1966) for Gadwall (*Anas strepera*) nesting mainly in nettles on an island at Lower Souris National Wildlife Refuge, North Dakota. Boyd and Campbell (The Wildfowl Trust, 18th Ann. Rept. 36-42, 1967) reported finding 268 Mallard nests on an 105-acre island in central Scotland in 1966.

We wish to thank Harold F. Duebbert for his suggestions and helpful criticism of the manuscript.—ROD C. DREWEN AND LARRY F. FREDRICKSON, *South Dakota Department of Game, Fish and Parks, Aberdeen, South Dakota (RCD) and Brookings, South Dakota (LFF)*, 17 March 1969.

Courtship display observed between two species of buteos.—The following details of courtship behavior between two species of *Buteo* were recorded by Frank Kish, Associate Curator at the Topeka Zoo.

The two flight cages for raptors at the Topeka Zoo are made of two regulation baseball backstops which have been joined together. The interior of each has several perches and two shelter boxes $2\frac{1}{2} \times 2 \times 2$ feet which are open in front and have no bottom. A perch is located within each box. In the cage concerned in the observations, one of these boxes is located beneath an oak tree growing outside of the enclosure. The tree would make the box more desirable as a nest site offering "concealment" and protection from the elements. On 2 January 1968 two adult Red-tailed Hawks (*Buteo jamaicensis*), a male and a female, one adult male Swainson's Hawk (*Buteo swainsoni*), and an adult male Harlan's Hawk (*Buteo harlani*) were in this enclosure. The male Red-tail had suffered a broken wing and could not fly at all well. Both Redtails were

local birds (northeastern Kansas) and the Swainson's Hawk and Harlan's Hawk had been shipped from Calgary, Alberta, Canada. All of these birds lived in harmony together. In mid-January, courtship displays between the female Redtail and the male Swainson's Hawk began and lasted approximately one month.

The female Redtail's displays consisted of inviting the male Swainson's by calling and wing-flapping, to the shelter box which seemingly she had come to regard as a nest. The male Swainson's responded by flying over and landing on the box beside her. The female tried to solicit the male by spreading the feathers covering the cloaca and by lifting her tail. This type of display occurred quite frequently and was more intensive in the morning. No food begging, courtship feeding, or nest building was seen. The male responded only by perching next to the female and no copulation was ever observed.

On 26 January 1968, several weeks after the commencement of the female Redtail's displays, a new healthy male Redtail was introduced into the enclosure. This bird had been hand-raised from a day-old nestling and subsequently trained to the glove after the manner of falconers. The bird, thus raised and tamed was more easily intimidated by other birds. The female Redtail attacked the new male so frequently that he was removed on the following day.

It is highly unlikely that such courtship behavior would occur in nature because of the abundant choice of mates of their own species presumably available to free-ranging birds. A. P. Gray (Bird hybrids, A check list with bibliography, Commonwealth Agricultural Bureau, Farnham Royal, Bucks, England, 1958) indicates that definite, proven hybrids between hawks in general and Buteos in particular are rare and that no cases of hybridization between *B. jamaicensis* and *B. swainsoni* are known.

We would like to thank Gary K. Clarke, Director of the Topeka Zoo, for permission to publish this material, and Robert M. Mengel, of the University of Kansas Museum of Natural History, for critically reading this paper.—BRUCE R. WOLHUTER, *University of Kansas Museum of Natural History, Lawrence, Kansas* AND FRANK KISIL, *Topeka Zoological Park, 632 Gage Boulevard, Topeka, Kansas, 29 November 1968.*

Food habits of wintering Sparrow Hawks in Costa Rica.—Sparrow Hawks (*Falco sparverius*) begin arriving in Costa Rica from the north in August or September. Some remain there for the winter, occupying the more open habitats, often those under cultivation or cleared for pasture. They depart for the north about April of the following spring. My observations show that during this period they are solitary, apparently territorial and, once in possession of a sufficiently food-rich territory, absolutely sedentary. I recorded several wintering individuals which could invariably be found on their territories and in the vicinity of a few favored perches throughout their stay.

A male bird which arrived on the grounds of the Inter-American Institute of Agricultural Sciences near Turrialba about mid-October, 1967, disappeared on 29 March, 1968. It took up residence in an area about 400 m in diameter which it never left. Usually it could be found along some electric power lines which crossed the area, either perched on the wires or on the tops of the poles. The area was bisected by a paved road parallel to the power lines. One side of the road was occupied by hedged lawns and a short-grass horse pasture; and on the other side was a wet pasture with rank grass, scattered trees, and overgrown fencerows.

The hawk hunted primarily on the lawns and horse pasture, where it generally dropped directly onto its prey from a perch. When it hunted over the high grass, it frequently hovered on the wing after the kestrel fashion. I recorded 97 successful prey captures

out of 246 attempts. All prey were captured on the ground. In 41 cases, the prey item was positively identified through binoculars or by the examination of fragments dropped in feeding. Of the identified items, 9 were short-horned grasshoppers (Acrididae), 19 were long-horned grasshoppers (Tettigoniidae), and 11 were lizards of the genus *Anolis* (probably *Anolis limifrons*). One item was a large cockroach (Blattidae) and the last was a small colubrid snake. This list is probably biased since grasshoppers and other large insects were difficult to identify at a distance but were abundant in the area. In about 30 cases where identity could not be certainly established, it appeared that the bird was tearing off wings as it characteristically did with large insects. The lizards and snake on the other hand, were easily distinguished by their long tails which hung down from the hawk's talons.

I recorded about thirty additional prey captures by other individuals wintering in the Turrialba area, but, because of the greater distance from the observer, only four of these could be identified. Two were *Anolis* lizards and one was a tettigoniid grasshopper. A good-sized *Ameiva* lizard (probably *Ameiva festiva*) was taken by a wintering female. *Ameiva* lizards were present on the territory of the male hawk at the Institute, but no captures were recorded. It may be that the significantly larger size of females permits them to take larger prey, but these few data are not sufficient to justify such a statement. No warm-blooded prey or attempts on warm-blooded prey were recorded. Suitable mammals are uncommon and the place that they occupy in the diets of hawks in the temperate zones is largely filled by the abundant reptiles and large insects. Birds are not molested by wintering Sparrow Hawks and show no great fear of them, often perching on the same tree or power line.

These observations were made while the author was engaged in a study of avian ecology supported by a Harvard University Scholarship, NSF grant number GB7346 (Reed C. Rollins, principal investigator), and by a grant-in-aid of research from the Society of Sigma Xi.—ROBERT E. JENKINS, *Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, 13 February 1969.*

Marsh Hawk chases crows mobbing owl.—On 5 November 1968, at 08:00, near Shabbona, DeKalb County, Illinois, I observed a Great Horned Owl (*Bubo virginianus*) that was perched on the ground near the edge of a partially picked corn field. A drainage ditch paralleled the border of the field and a dense growth of annual weeds, grasses, and willows (*Salix* sp.) extended for about 30 feet on both sides of the waterway. My attention was directed to the owl by the raucous calls of eight Common Crows (*Corvus brachyrhynchos*) that were mobbing it.

After the crows had been swooping at the owl and calling almost continuously for about four minutes, the owl flew toward the ditch and landed on a fence post. The crows' activity seemed to become intensified during the owl's short flight. Four of the crows landed on fence posts, all in the same direction from the owl, and the others continued flying about near the owl and calling. About two minutes later a female-plumaged Marsh Hawk (*Circus cyaneus*) flew in low over the adjacent corn field and briefly chased each of the four flying crows. The crows maneuvered swiftly and left the immediate area. The hawk then dived at each of the perched crows and caused them to fly. All eight crows flew to a row of large trees about $\frac{1}{4}$ mile north and landed. The hawk left the area immediately and disappeared to the west (08:08). Approximately one minute later the owl (possibly in response to my presence) flew for about 200 yards and landed on the ground in a hay field.

At 08:12 the crows arrived at the owl's new location and resumed mobbing activities. Within two minutes a Marsh Hawk appeared from out of the west and chased each crow for a brief period. The crows quickly departed to the north and the hawk flew west (08:15). Neither species returned to the hay field during the next 45 minutes.

The significance of this observation cannot be determined at this time. It seemed that the Marsh Hawk was attracted by the noise generated by the mobbing crows; however, the hawk did not return after its second departure when the same crows mobbed two Short-eared Owls (*Asio flammeus*) that were flying over a hay field $\frac{1}{4}$ mile north of the Great Horned Owl's location.—WILLIAM E. SOUTHERN, *Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, 23 January 1969.*

Ruddy Turnstones making use of Yellow-crowned Night Herons for food-finding.—On 5 June 1948 I was watching a number of Yellow-crowned Night Herons (*Nyctanassa violacea*) feeding on the innumerable crabs on the coastal mudflats at the mouth of the Coppename River, Surinam. Near one of them stood two Ruddy Turnstones (*Arenaria interpres*) which swallowed the remains of a crab which fell out of the heron's bill on the mud. The turnstones obviously watched the feeding herons as each time a heron captured a crab they hurried toward the feeding bird and swallowed the wasted morsels as soon as they fell on the mud. The turnstones never chased or bothered the herons but simply waited their turn and the herons apparently did not take any notice of them.—F. HAVERSCHEIDT, *Wolfskuilstraat 16, Ommen, Holland, 29 March 1969.*

Common Terns pirating fish on Great Gull Island.—In 1967, while working in the Great Gull Island tern colony, located 7 miles ENE of Orient Point at the eastern end of Long Island, New York, I saw adult Common Terns (*Sterna hirundo*) pirating fish brought in to feed the young. An adult would fly in carrying a fish. The young tern would rush out, grasp the fish in its bill and at that moment a second adult Common Tern would dart in and make off with the fish. The young, still holding the end of the fish, would be lifted 8–10 feet in the air, then would drop to the ground without the fish. The fall did not seem to hurt the young tern. Pirating of Common Terns by Common Terns was seen on several occasions, but I did not see this pattern in Roseate Terns (*Sterna dougallii*) which also nested on the island. In the three years I have worked on Great Gull Island I have seen pirating only in 1967.

Bannerman (*Birds of the British Isles*, p. 152, 1962) reports Roseate Terns in the Farne Islands as pirating fish regularly from Arctic Terns (*Sterna paradisaea*).

Austin (*Bird-Banding*, 5:155–171, 1934) states that the degree of food abundance for a tern colony can be estimated from the number of fish found on the ground in the colony during the season. Using this criterion the bait fish, on which the terns feed were in short supply in our area in 1967. In contrast to 1966 I found very few fish on the ground near these nests and less variety in those I did find: 3 species in 1967, in contrast to 9 species in 1966. In 1968 not many fish were found in the colony, but growth rate studies of the young Common and Roseate Terns on the island (LeCroy and Collins in prep.), suggest the food supply was better in 1968 than in 1967.

As far as I know there are no data on relative abundance of bait fish for this area for the period 1966–1968. Dr. William A. Lund, Jr., working on bluefish (*Pomatomus*

saltatrix) in areas near Great Gull Island reports (pers. comm.) his impression that 1966 was a good year for bait fish, in 1967 bait fish were very low and in 1968 they were more abundant. Bluefish and terns are often seen feeding in the same areas, the fish chasing the bait to the surface where the terns dive for it.

Since pirating of fish by Common Terns seems to be exceptional in the Great Gull Island colony, its occurrence may have been correlated with a shortage of bait fish. Where pirating is seen regularly, as described for the Farne Islands Roseate Terns the pattern may have had its beginning during a period when bait fish were in short supply.—HELEN HAYS, 14 East 95th Street, New York, New York 10028, 5 March 1969.

Sand-kicking camouflages young Black Skimmers.—Bent (U.S. Natl. Mus. Bull., 113:315, 1921) describes young Black Skimmers (*Rynchops nigra*) digging themselves into depressions on the beach when disturbed. "From their earliest stage the young skimmers have a habit of scratching themselves into a hollow and lying absolutely flat upon the shell-covered beach. While this habit is displayed mostly by the downy young, I have seen it exhibited to a great extent by the feathered young when the young birds are able to run about and danger threatens. Then they will throw themselves flat on the shells of the beach and scratch alternately with their little webbed feet backward. They make 15–20 movements before they snuggle down to rest, and while their legs are in action they make the shells fly most energetically. When the hollow is dug sufficiently to allow them to lie flush with the surrounding beach they remain absolutely motionless. . ." Stone (Bird studies at old Cape May, II:604, 1937) mentions the difficulty of seeing young skimmers as they lay in depressions with sand apparently drifted around them.

On 7 August 1968 we visited a sand bar in Shinnecock Bay at the eastern end of Long Island, New York, where terns and skimmers nest. As we walked into the colony we saw spurts of sand ahead of us. As we approached the sand stopped flying and there would be a young skimmer lying very still, partially covered with sand.

On 27 August 1968 we visited a section of beach about one mile south of Stone Harbor, New Jersey where skimmers were nesting. We found a nest where one egg had hatched and two eggs were still left in the nest. The young skimmer, which looked at most a day old, was still kicking sand into the air as we stood over it. The sand fell on the back of the bird.

The sand-kicking as Bent suggests does function in digging a depression in which the bird lies. It seemed to us equally important, however, that the sand which is kicked into the air falls on the back of the young skimmer partially covering it, and from our point of view, at least, helping to camouflage it. It seems likely that Stone's drifted sand could have been sand kicked by the young skimmers. The camouflage aspect of this kicking may not be realized if the substrate is composed of small stones, or shells, which the young skimmer could not easily kick into the air.

Conway and Bell (Living Bird, 7:57–70, 1968) describe Kittlitz Sandpipers (*Charadrius pecuarius*) kicking sand over their eggs when disturbed. We have not found any reference which suggests the camouflage function for sand-kicking in young skimmers, but feel it is applicable.—HELEN HAYS, 14 East 95th Street, New York, New York 10028, AND GRACE DONALDSON, Department of Education, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, 27 February 1969.

Barn Owls hunting by daylight in Surinam.—In my "Birds of Surinam" (1968) I stated that the local race of the Barn Owl (*Tyto alba hellmayri*) in Surinam is strictly nocturnal. Since writing this I have twice observed a Barn Owl hunting by daylight.

On 11 June 1967 I saw one at 11:00, in bright sunlight, quartering the open and sandy savanna bordering the runway of the airfield at Zanderij. When the bird came nearby I collected it. It was a male in non-breeding condition and it had only a small lizard (Teiidae) in its gizzard. Its weight was only 387 grams. Eleven other specimens from Surinam averaged 486 g (extremes 410–558 g).

On 9 February 1968 at 10:00, once more in bright sunlight, I watched a Barn Owl hunting along the dam through a newly planted citrus plantation near Paramaribo. Three times it pounced down on the grassy roadside but it missed its prey each time. I am sure that it was chasing lizards which were numerous on the roadside.—F. HAVERSCHEMIDT, *Wolfskuilstraat 16, Ommen, Holland, 29 March 1969.*

Food preferences of a hand-raised Blue Jay.—The kind of food that a Blue Jay (*Cyanocitta cristata*) eats depends largely upon the kind available in a given locality at a particular time of the year (Dyche, Trans. Kansas Acad. Sci., 21:130–137, 1908). Beal (USDA Yearbook 1896:197–206, 1897) examined 292 Blue Jay stomachs and Dyche (op. cit.) examined over 150 stomachs. Both authors agreed that approximately 24 per cent of the total yearly diet consisted of animal food (mostly arthropods) while 76 per cent was plant material (predominantly seeds and accessory structures). Good-

TABLE 1
PLANT PRODUCTS CACHED OR EATEN BY RB 2 IN ADDITION TO REGULAR DIET.

Plant & Plant Products Sampled	Preference	Plant & Plant Products Sampled	Preference
Peas	+++	Coffee (cream)	+
Onions	+	Coffee (sugar)	++
Bean sprouts	++	Tea (any form)	+
All green vegetables	+	Carbonated soft drinks	–
Pineapple*	–	Beer (stale)	+++
Banana	+	Beer (fresh)	+
Blueberries	+++	Other alcoholic beverages	–
Raspberries	++	Candy & granulated sugar	+++
Strawberries	+	Peanuts	+++
Cooked fruits & fruit desserts	+	Almonds	++
Oranges & orange juice	+++	Acorns	–
Grapefruit & juice	+	All other nuts	+
Lemons & juice	+	Popcorn	++
Sweetened fruit juices	++	Potato chips	++
Pickle juice	+++	Tobacco	+++
Coffee (black)	–	Paper**	+
Coffee (cream & sugar)	+++	Houseplants & cut flowers	++

– = not eaten or cached
 + = eaten or cached infrequently when available
 ++ = eaten or cached regularly when available
 +++ = eaten or cached with great frequency when available
 * Whole pineapples were mobbed.
 ** Paper was eaten only when it accompanied a preferred item.

TABLE 2
ANIMAL PRODUCTS CACHED OR EATEN BY RB 2 IN ADDITION TO REGULAR DIET.

Meat & Animal Products Sampled	Preference	Meat & Animal Products Sampled	Preference
Beef, lamb, fish & fowl	+++	Fats	+++
Mild sausages	++	Soap (coarse-milled, unperfumed)	+++
Bacon, cooked & crisp	+++	Soap (fine-milled, perfumed)	+
Bacon, unecooked or soft	+	Leather	+
Spicy sausages & meats	+	Dandruff	++
Butter	++	Cerumen	++
Margarine	+	Toothpaste	++
Milk	-	Bee & candle wax	+
Eggs	+++		
Egg shells	+++		

- = not eaten or cached
 + = eaten or cached infrequently when available
 ++ = eaten or cached regularly when available
 +++ = eaten or cached with great frequency when available

win (Avicult. Mag. 59:122-133, 1953) observed that his captive Black-throated Jays (*Garrulus lanceolatus*) sampled a wide variety of plant and animal food offered to them.

During a behavioral study of Blue Jays in 1962-1964, a hand-reared male Blue Jay (RB 2) kept at home was given a regular diet of canned dog food, cuttlebone, cooked chicken eggs, raw beef liver, live insects, an insectivorous bird mixture developed by Ficken and Dilger (Avicult. Mag. 67:46-55, 1961), French's parrot mixture, cracked corn, peanuts, and suet. Since this bird was allowed to fly freely about the house, he was able to supplement his normal daily ration with food items not ordinarily available to jays in the wild, except perhaps those in picnic areas of parks. RB 2 sampled everything my family ate as well as a number of things we did not ordinarily eat (Tables 1 and 2). Some items were always eaten or cached by RB 2 when available and others were less regularly eaten or cached, and a preference order seemed to become established for the variety of items which were eaten. RB 2 seemed to recognize colors and shapes of wrappers and packages of his preferred items.

If one regards RB 2's feeding behavior as indicative of the feeding behavior of wild jays, one could infer that jays sample a very wide range of possible food sources, eating selectively from the items sampled and establishing definite food preferences.—A. R. WEISBROD, *Division of Biological Sciences, Cornell University, Ithaca, New York 14850, 17 March 1969.*

A White-throated Sparrow nest in western Pennsylvania.—The first nesting record for the White-throated Sparrow (*Zonotrichia albicollis*) in western Pennsylvania was made when I found a nest containing 2 eggs in McKean County on 13 July 1968. Todd (Birds of western Pennsylvania, 1940) recorded summer sight records from 1929 to 1937 at Hearts Content in Warren County, in northwestern Crawford County, and twice at Pymatuning Swamp in Crawford County. A nest was found in the Ohio part of Pymatuning Swamp in 1932, an area since flooded by a reservoir. It was reported to be casual in summer near Dubois and "may breed occasionally." On a map showing summer records of the White-throated Sparrow in Pennsylvania, Poole (Pennsylvania birds—an annotated list, 1964) indicated these localities listed by Todd as implied nestings.

The nearest previous nesting record for Pennsylvania was in Sullivan County in north-eastern Pennsylvania, about 110 miles from the new locality. The nearest nesting locality in New York is about 60 miles north at Java Lake Bog, Wyoming County, where two adults and two young were found (Beardslee and Mitchell, *Birds of the Niagara frontier region*, 1965).

The McKean County locality is a swamp of some 60 to 100 acres in the center of the county. The swamp lies in a broad, shallow basin on the unglaciated plateau at an elevation of 2,100 feet, and is predominantly a shrub swamp with little or no marsh or bog, although sphagnum moss is widespread. Among the most abundant shrubs are arrow-wood (*Viburnum recognitum*), wild raisin (*Viburnum cassinoides*), black chokeberry (*Aronia melanocarpa*), and low sweet blueberry (*Vaccinium angustifolium*). Hemlock (*Tsuga canadensis*) is the most abundant tree species. Many of them are small and have a peculiar, dense, closely-sheared appearance resembling krummholz.

The nest had been built at the base of a clump of wild raisin surrounded by a patch of low sweet blueberries 2 to 3 feet in diameter, and all of this was raised about 6 inches above the surrounding sphagnum. There was a large clump of small hemlock trees nearby, and an open stand of shrubs and small hemlocks in other directions. The nest was made almost entirely of fine grasses or sedges. The outside diameter was about 3.5 inches, the inside diameter 2.4 inches, and the depth of the cavity 1.5 inches. The 2 eggs were pale bluish and heavily spotted with brown. There were fine markings on the small end, but the large ends were nearly solid brown with a few dark purplish marks. They measured 20.2×16.5 millimeters. This probably represents a second nesting, considering the very late date (Lowther and Falls *in Bent*, U.S. Natl. Mus. Bull. 237, 1968).

The population of White-throated Sparrows in this swamp has been fairly consistent with a minimum of 5 or 6 pairs each summer since 1965, when I found the colony. Other species found here in summer include several of the more common birds with northern affinities such as the Hermit Thrush (*Hylocichla guttata*), Canada Warbler (*Wilsonia canadensis*), and Slate-colored Junco (*Junco hyemalis*) and the scarcer Nashville Warbler (*Vermivora ruficapilla*).—TED GRISEZ, 8 Belmont Drive, Warren, Pennsylvania, 24 March 1969.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

During the past year gifts have been received. From:

Reeve Bailey—3 bulletins	Douglas M. Lay—15 reprints
Richard C. Bjorklund—1 reprint	Alice Miller—26 books, 24 journals, 20 reprints, 32 wildlife prints
William H. Burt—29 journals, 9 reprints	Margaret M. Niece—1 bulletin, 4 reprints
John Check—2 reprints	Olin S. Pettingill, Jr.—1 book
Frank B. Gill—3 books, 4 reprints	William Russell—1 book
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F. N. Hamerstrom, Jr.—1 book, 26 reprints	Robert W. Storer—2 journals, 43 reprints, 1 report
Emmet Hooper—1 reprint	Harrison B. Tordoff—2 journals
David W. Johnston—2 books, 26 reprints, 1 translation	Lars von Haartman—1 book, 2 reprints
Leon Kelso—1 book, 3 translations	John E. Willoughby—215 journals
S. Charles Kendeigh—5 reprints	Martha S. Wilson—1 book
Peter H. Klopfer—9 reprints	Larry Wolfe—2 reprints
Robert C. Lasiewski—1 reprint	Howard F. Young—6 reprints

ORNITHOLOGICAL NEWS

Ernest Mayr, of Harvard University, was one of the six distinguished scientists, and the only biologist, awarded the National Medal of Science for 1969 by President Richard M. Nixon.

The Society's First Vice-President, Pershing B. Hofslund was awarded the Thomas Sadler Roberts award for contributions to Minnesota ornithology by the Minnesota Ornithologists' Union.

Members planning on attending the annual meeting in Colorado may be interested in the recent publication: "Birds in Western Colorado," an annotated field list and travel guides for finding the best birding spots obtainable from the Historical Museum and Institute of Western Colorado, 4th and Ute Streets, Grand Junction, Colorado 81501. \$1.75.

The back cover of this issue of *The Bulletin* gives some information about the annual meeting, and should be read carefully by all those who might feel that Colorado is a distant location for the meeting. The opportunity of meeting with our sister society, the Cooper Society is one that many of us have looked forward to for some time. The ornithological attractions of the region are most enticing, and your Editor, who has spent parts of 8 summers in Colorado, will testify that the many other attractions of the state are equally inviting.

THE RING'S INDEX ORNITHOLOGORUM

The editor of the *International Ornithological Bulletin* THE RING proposes to publish an *Index Ornithologorum* embracing the professional and amateur ornithologists of the world.

All entries should be in English and should be accompanied by one International Postal Reply Coupon for further correspondence. Closing date for all entries is June 30, 1970, but earlier arrival of entries would be appreciated. Do not delay—send your entry to-day.

The address is: The Editor, THE RING, Laboratory of Ornithology, Sienkiewicza 21, Wrocław, Poland.

An entry (in English) should contain the following information:

1. Surname
2. Names in full
3. Year of birth (optional)
4. Title
5. Positions held (including editorships, memberships, etc.)
6. Principal interest in ornithology
7. Address
8. Authors of ornithological publications are requested to quote the most important of them.
9. Do you intend to purchase a copy of the INDEX if reasonably priced?
10. One I.P.R. Coupon is enclosed: yes—no. Date. Signature.

ORNITHOLOGICAL LITERATURE

PEREGRINE FALCON POPULATIONS: THEIR BIOLOGY AND DECLINE. Edited by Joseph J. Hickey. University of Wisconsin Press, Madison, 1969; 6½ × 9¼ in., xxii + 596 pp., 32 pages of photos. \$10.00.

The difficulty of reviewing this work can be briefly summarized by noting the fact that the book consists of 32 individual articles, nine discussion sections, and 12 brief reports on other raptors. It is the proceedings of an international conference held in the fall of 1965 to discuss the unprecedented decline of the Peregrine during the previous decade. Rapid publication of a conference of this type is difficult, due to the large number of contributors; in this respect this work compares unfavorably with the proceedings of the International Ornithological Congresses. This is to be regretted in such a rapidly developing field as the relationship of wildlife to environmental change. However, some of the most significant findings to 1968 have been added to the discussion.

The first 280 pages are devoted to population studies of the Peregrine. In Alaska and British Columbia no change in the Peregrine population has been found. This is probably true for the northern Canadian population, estimated at 7,500 pairs, although detailed data are lacking. In the western United States the population has been seriously reduced and the species has been extirpated from the eastern United States. In Europe the decline has been most severe in the northern and central areas. The current Finnish population being only a few percent of their former numbers. In West Germany a decrease of 77 percent between 1950 and 1965 was noted. In the British Isles an unprecedented decline started in the mid 1950's but the population has now apparently stabilized at a low level. In France the Peregrine has been extirpated in Normandy and severely reduced elsewhere. The continued success of the species in Spain, only briefly noted in the conference, is the one bright spot in Europe. No information is presented for Russia or southeastern Europe.

The conference discussed a wide range of possible explanations for the decline. This can be divided into two parts, a slow long-term decline due to the encroachment by man and a rapid decline over wide areas starting in the early 1950's. The rapid decline in various areas had at least some of the following characteristics in common: (1) failure to lay eggs, (2) reduced clutch size, (3) egg breaking and eating, (4) failure to re-lay after loss of initial clutch, (5) embryonic mortality, and (6) some nestling mortality. Hickey and Roelle conclude (p. 565) that "The ecological case against the chlorinated hydrocarbon insecticides as the pervasive factor in these phenomena is essentially complete." While this view is a fair summary of the viewpoint of the conference, some of the inconsistencies of the data are discussed at length by Stickel in Chapter 42. Nor are other possible factors neglected. Pathogens, parasites, and predation are discussed but no evidence for these factors causing a serious widespread decline was found.

The plates are well chosen to show nest sites and habitats. Many are, I believe, not previously published although the editor was unable to resist the inclusion of the most famous Peregrine photograph of all—A. A. Allen's Peregrine at Taughannock. Reproduction is adequate but not first class. The figures are well drawn and the index excellent. Typographic errors appear to be few, although I had difficulty in deciding what I had done on elucidating the mechanism of change of calcium metabolism (p. 564). On the subject of style, one can say little since so many contributors are involved. The term "decimating factors" referring to the northern Canadian population is surprising, considering the apparent stability there. Decimating means literally the

killing of every tenth individual. Would that the eastern population of the Peregrine had merely been decimated!

In view of the enormous interest in oil in Alaska, one imagines that there is no prospect of Cade's visionary idea (p. 504) of the setting aside of a wilderness area coming to pass. Future generations will regret that his suggestion for the minimum requirement for preservation, "the setting aside of the entire Arctic Slope of Alaska as a wilderness refuge and the restriction of any permanent human habitation north of the Brooks Range" including the entire upper Yukon drainage system, was not acted on.

Not only ornithologists but all persons interested in conservation are in Hickey's debt for his work on this conference and its proceedings. The value of examining changes of the environment on a greater than national basis are clearly shown.—DAVID B. PEAKALL

A DISTRIBUTIONAL SURVEY OF THE BIRDS OF HONDURAS. By Burt L. Monroe, Jr. Ornithological Monographs No. 7, American Ornithologists' Union, 1968: 458 pp., 2 col. pls., 28 text maps. \$9.00 (\$7.20 to A.O.U. members).

This is the first comprehensive distributional account of Honduran birds. Hitherto Honduras has lacked even an adequate check-list, although zoogeographically the country is one of the most complex and interesting in Central America. The interior is believed to date back to Palaeozoic times, constituting part of "nuclear" Central America, which was separated from South America by water gaps in Nicaragua and Panama during most of the Tertiary. Since then many South American humid forest species have spread northward, but encounter an ecological filter barrier in the arid interior valleys and in the puzzling pine savannas of the Caribbean coast. These pinelands, of uncertain origin, have fostered an extension into the tropical lowlands, south to Nicaragua, of several temperate North American species, which farther north in Middle America inhabit highlands. The last check-list for Honduras (Stone, 1932) listed 410 species. My own Middle American list (1955), based largely on published records, attributed 585 species to Honduras, 11 of which Monroe, very properly, doubts or rejects. He accredits 663 species to Honduras, including the Swan Islands. One may question the inclusion of the avifauna of these islands, some 200 km out in the Caribbean, as an integral part of that of Honduras—considering the fact that the United States has long exercised jurisdiction as sovereign. But the species added consist only of a few West Indian endemics and migrants from the north.

Although not stated, this work is essentially Monroe's doctoral dissertation at Louisiana State University. Judging by literature references to 1966, some subsequent changes were made. Monroe collected in Honduras from 2 August 1962 to 13 May 1963, and from 30 March to 19 April 1964; he also had available specimens obtained by other field parties from his university. The most important material studied consisted of the vast collections made by the professional collector, C. F. Underwood, between 1931–1938, numbering well over nine thousand skins, scattered in various museums. Monroe checked most of Underwood's birds, including those in the United States and in the British Museum, as well as significant collections made by others. With this material, his field experience, and his investigation of the literature, Monroe has been able to provide a better picture of bird distribution in Honduras than is presently in print for the neighboring countries of Guatemala and Nicaragua. He points out that Honduras is still perhaps the least known country in Central America and that several areas have not been worked at all or very superficially. Much of this rugged country is devoid of roads

and accessible only with difficulty. Some taxonomic problems involving distribution will require for their solution detailed field studies concentrated on particular species. But Monroe provides a good start.

The work is carefully organized. Two color plates by his university colleagues, S. A. Gauthreaux, Jr. and J. P. O'Neill, adorn the book. There are many helpful text maps. An introduction emphasizes the zoogeographic importance of Honduras, reviews recent additions to the known avifauna, and indicates areas particularly needing ornithological exploration. Then follows treatment of geology, soils, climate, and habitats. For habitats Monroe adopts essentially the nomenclature of Carr (1950); my only question here is the inclusion under "rain forest" (the wettest forest class) of areas with as little rainfall as 80 inches per year. A section entitled "History of Honduran Ornithology" includes, *inter alia*, not only Monroe's itinerary, but a useful summary of Underwood's travels. The central and major part of the book consists of individual species accounts. Under a species heading, with scientific binomen and English name (based on Eisenmann, 1955, or the A.O.U. Check-List, 1957), are listed Honduran specimens examined, giving number, locality, sex, date, and institution where housed; then additional published locality records. A paragraph or two summarizes Honduran distribution, habitat, and status. Where appropriate this may be followed by a comment on taxonomy at the species or genus level. A final paragraph "Geographic Variation" discusses the subspecies to which Honduran specimens should be attributed, not infrequently rejecting a described race. At the end of the book are interesting accounts of migration, an analysis of the avifauna by habitat and by presumed origin, a gazetteer, a bibliography, and an index.

Monroe intentionally has restricted this book to systematics and distribution, giving very little data on behavior, life history, or details of ecology. He has thus been able to devote considerable space to discussion of taxonomy at the species and subspecies level. I do not feel competent to appraise the question of Honduran subspecies; but, on the species level, generally I find myself in agreement, and where my present opinion may differ, the case admittedly is a controversially uncertain one.

As Monroe has been exceptionally careful in regard to nomenclature, it may be appropriate to call attention to a few such matters. The original spelling of the subspecific name of *Cypseloides rutilus brunnetorques* (Lafresnaye), which is used by Peters and Zimmer, should be maintained; the emendation, "*brunnetorques*," formerly often seen, is not warranted by the Code. I share Monroe's objection to the recently suggested transfer of this name from the Colombian form to the west Mexican race (long known as *griseifrons*), on the basis of re-identification of an ancient, faded, mounted specimen. Monroe's rejection on the ground of *nomen oblitum* of the proposal (Deignan, 1961; Phillips, 1962) to supplant the well-known *Chaetura richmondi* Ridgway by "*Chaetura similis* Salvin and Godman," is correct, but "*similis*" can be rejected for a more basic reason, that it is not an "available" name under Code, Art. 11(d), as has been pointed out by Wetmore (1967). Following all authors since Stone (1897), including Ridgway (1902) himself, Monroe has treated the original spelling of the subspecific name *Sturnella magna inexpectata* Ridgway (1888) as a *lapsus* for *inexpectata*. R. W. Diekerman has kindly called to my attention that, according to Latin dictionaries, either spelling was correct, hence no *lapsus* justifying emendation could be assumed. Nevertheless, the fact that Ridgway himself in his major work (1902) intentionally adopted Stone's emendation is evidence that the original spelling was in fact inadvertent; the same uniform usage by others for seventy years justifies its maintenance by Monroe. Monroe accepts Stein's specific division of the *Empidonax traillii* complex, and (following Stein) uses the name *E. brewsteri* Oberholser for the populations which

call "fitz-bew." For reasons to be detailed elsewhere, I believe that (regardless of specific or subspecific status) Audubon's name *traillii* belongs to the Arkansas prairie population, which is a "fitz-bew" vocalizer, and *alnorum* Brewster to the northern "fee-bee-o" singers.

On many controversial matters of taxonomy, Monroe has not hesitated to express his opinion, sometimes in unequivocal terms, but at least he has given his reasons. He explains his philosophy, which he states will cause him to be regarded as a "splitter" at the generic and specific levels and a "lumper" at the subspecific level. Actually he has done no new splitting in this book, but merely rejected some recent proposals for lumping genera and species. His conservative approach will not endear him to those ornithologists who are sensitive about the sinking of their subspecies or who feel strongly about their taxonomic views. As an author of a distributional work has to select the scientific name to use, he is forced, at least to that extent, to make a taxonomic decision in controversial cases. The systematic investigation necessary to determine local subspecies usually is feasible in a regional study, but when it comes to taxonomic problems at the generic or species levels whose determination may require going far beyond the area treated, most authors dealing with local distribution feel it the safer course to rely on some published authority. Monroe not infrequently indicates that he has exercised a personal judgment; one cannot help wondering in certain cases how he had the time to investigate adequately the extra-Honduran material during the course of a Ph.D. study. Nevertheless, it should be said that his treatment of controversial genera and species is almost always in accord with that of the major neotropical taxonomists, Hellmayr, Peters, or Zimmer, and usually of all three. However, two cases are worth mentioning where, while Monroe may well prove to be right in his conclusions, he seems to me to oversimplify a problem whose satisfactory solution requires further fieldwork outside of Honduras. These cases warrant discussion, because Monroe's treatment, while deviating from that of most recent authors, is adopted in the recent Volume 14 of the "Check-list of Birds of the World" (1968), of whose section on Parulidae, Lowery and Monroe are authors. In agreement with Slud (1964), Monroe has removed the Buff-rumped Warbler, *fulvicauda* group, from the genus *Basileuterus* to *Phaeothlypis*, a genus erected by Todd (1929). In appearance, song, general behavior, and habitat, as Monroe indicates, this complex differs strikingly from other Middle American species assigned to *Basileuterus*. But the generic situation in South America, not here discussed, makes more dubious the recognition of *Phaeothlypis*. The South American *rivularis* group, found east of the Andes, which Todd expressly kept in *Basileuterus*, and excluded from his genus *Phaeothlypis* by the diagnosis provided, is so like the *fulvicauda* group in appearance and habits that all current authors regard the two as strictly congeneric, and many as conspecific. At most they are allopatric semispecies. As Monroe includes *rivularis* in *Phaeothlypis*, should not a new diagnosis be supplied of the enlarged genus that will separate it from *Basileuterus*? But the case is still more difficult. There are one or two other South American species that seem in appearance, and, judging from the literature, in behavior, and style of song, to bridge the gap between the *rivularis-fulvicauda* super-species and the more "typical" members of the genus *Basileuterus*. This is frankly indicated in footnotes in the Check-list of Birds of the World (1968, vol. 14, p. 75); so what are the distinguishing characters of *Phaeothlypis*?

Monroe merges *Basileuterus delatirii* with its more northern ally *B. rufifrons*, suggesting that they intergrade through *salvini* (which most authors have regarded as a race of *B. rufifrons*). On morphology this seems an acceptable treatment, and was adopted by Ridgway, but subsequently both Todd (1929) and Griscom (1932), with more material, insisted that the distribution in Guatemala showed overlap without intergradation. As

Monroe attributes all Honduran specimens to nominate *delatirii*, they contribute little to solution of the problem. Admittedly (as earlier pointed out by Dickey and van Rossem), Todd's supposed "generic" character of wing/tail ratio does not hold, but there are color differences that distinguish *B. delatirii* from the *B. rufifrons* group and may serve as specific characters if there is sympatry. Quite possibly the seeming overlap in Guatemala may be explicable by something other than sympatry, but that will require fieldwork there. The statement that the allied forms "are essentially allopatric and intergrade over a wide area in eastern Guatemala" imports a demonstrated fact, rather than an opinion as to probabilities. In this connection it should be noted that the traces of white below the auriculars reported in a few Honduran *delatirii* do not necessarily indicate introgression of *salvini* genes, for the same traces are often found in the distant subspecies *B. d. mesochrysus*, all the way to Colombia. These comments are not intended to discourage expression of opinion (a keen mind like Monroe's may have sound insights even on scanty data), but rather to encourage additional investigation of an open problem that might otherwise seem to be solved.

Anyone interested in the distribution and taxonomy of neotropical birds will find this a useful and stimulating (and sometimes controversial) book. If we had as conscientiously and competently prepared works for all countries of Middle America, the task of those preparing the next A.O.U. Check-List of North American Birds would be greatly facilitated.—EUGENE EISENMANN.

THE AUDUBON ILLUSTRATED HANDBOOK OF AMERICAN BIRDS. By Edgar M. Reilly, Jr. O. S. Pettingill, Jr., Editor in Chief. Sponsored by the National Audubon Society; published by McGraw-Hill Book Company, New York, 1968: 8¾ × 11¼ in., xvii + 524 pp., 31 col. pls., c. 400 bl. and wh. photos, 100 drawings. \$25.00.

This "handbook," which weighs almost five pounds, hardly fits my dictionary's definition, "a small book . . . for guidance." It is, instead, a heavy compendium covering all the birds that regularly occur in the United States and Canada, including Greenland, Alaska, and Hawaii. It also treats, but usually in less detail, extinct birds, introduced species, and accidentals for which specimen records exist: a grand total of nearly 875 species.

After a brief introduction, the book takes up each family in A.O.U. Check-list order, the Hawaiian forms interspersed with the North American. The families are introduced by a brief summary of their characteristics: body sizes, general plumage types, geographical ranges, breeding data, interesting extralimital forms, etc. This general summary is then followed by a separate account of each species in that family. Some birds are covered by a short paragraph or two, but most are given a more thorough treatment, organized by seven topic headings: appearance, voice, range and status, habitat, seasonal movements, biology, and suggested reading. Well over 500 of the species are illustrated by photographs or drawings.

When an author sets out to discuss some 875 species in 505 pages, approximately one-half of which are filled by illustrations, his text must necessarily be written in a very condensed style. In most instances Reilly has done this very well. The least successful cases are in the plumage descriptions; they are very uneven, some too short (the Common Loon is given only five lines, and the adult breeding plumage is not described) and others overly long (McCown's Longspur rates 20 lines of painstaking description). A few are simply poor or confusingly worded (Brown Pelican) but the majority are

probably adequate for the space available. The voice descriptions are also spotty, some good, others inadequate in light of present knowledge. Reilly often fails to identify the behavioral implications of sounds, although they are generally available in recent literature: which vocalizations are territorial song, which alarm notes or distress calls, etc. Range (including extralimital) and status are described in considerable detail, much more than in most field guides. In places the very condensed geographical shorthand ("P.E.I." and "c.Mack.," for example) may be confusing to readers not used to this sort of thing, but it usually can be deciphered through adjacent, more familiar, abbreviations. The remarks on status are often very useful, but not always current; the figure given for Whooping Cranes is 33 in 1963.

By far the most valuable aspects of the book are the sections on seasonal movement, habitat, and biology. These contain information that is not usually in field guides and may be difficult to find without a sizeable reference library. Even if a reader has extensive library facilities available, it is extremely convenient to have migration times, habitat preferences, and such aspects of basic biology as number and color of eggs, incubation periods, fledging ages, and number of annual broods for all North American birds brought together in one volume. In the weeks I have had this book, I have used it often for this kind of information.

Reilly has been very careful in his compilation of data not to gloss over those aspects of avian biology that are not known. He clearly points out gaps in our knowledge of American birds and it is hoped that readers may fill these in as opportunities arise. I am sure that many facts, particularly incubation periods and fledging ages of some of our commonest birds, remain unrecorded simply because few people realize they are yet to be determined.

Overall, it is clear that this book has been painstakingly researched and compiled. It is a monumental collection of information, and as such, the author may be justly proud of the almost complete lack of factual errors therein. One of the few mistakes I spotted was the statement that only (adult) male Cedar Waxwings bear "the waxy scarlet tips on the smaller feathers of the wing"; adult females also occasionally have well-developed "wax" tips, and I have even seen small bits of red in the juvenal plumage.

Probably the greatest fault of the book lies in its writing style. Although it is encyclopedic in nature, and perhaps not meant to be read through like a book with a narrative, it is nevertheless exceedingly dull reading. Time after time I noted the omission of an interesting bit of information or mention of current exciting research that might have given the book some life. People study birds because they find them interesting; this compilation will offer facts about birds, but very little of what is fascinating about them.

The book also contains a large number of inconsistencies and small annoyances. Reilly lists the (editorial office) addresses of the three main American bird journals, but with no indication that these are temporary; indeed, two were out of date when the book was published (the A.O.U. in Lawrence, Kansas, and the Cooper Society in Berkeley, California). The Introduction states that the ranges will be given from west to east, and then the first one (Common Loon) is given east to west. Some of Reilly's discussions of family affinities are puzzling and need explanation, particularly such statements as "[swallows] are probably most closely related anatomically to the larks, thrushes, and weaver birds." And throughout the sections on Suggested Reading there is a lack of references to modern literature. Surely something more recent than John Burroughs' "Wake-Robin" (1871) could have been found for the Hermit Thrush? Two papers on the mating behavior of the Sage Grouse (Auk, 1940 and 1942) are the only references for

that species, missing the comprehensive monograph by R. L. Patterson in 1952. Obvious (and commendable) effort was made to keep to standard or easily-obtained literature, but exceptions occur (e.g., the title for the Greater Prairie Chicken is a University of Missouri publication) so there is no excuse for not including important references where they are pertinent and comprehensible to the general reader.

Primary among the inconsistencies, however, are the uneven treatments within and among certain species. To my mind there is too much general emphasis on "unusual" birds—accidentals and species with very restricted ranges. This may be an attempt to give better coverage to species that are usually omitted altogether from North American books, but it leaves this book out of balance. I cannot see why the White Ibis, a common enough bird in the southeastern states, is dismissed in only eight lines as "Essentially a white-plumaged Glossy Ibis . . .," which it is *not*; yet the introduced Spotted-breasted Oriole found only in the Miami, Florida region, deserves 29 lines. Sutton's Warbler, be it a hybrid or full species and on the Hypothetical List of the A.O.U. Check-list, is still in many of the field guides and deserves some mention, if only as an ornithological will-o'-the-wisp; both Brewster's Warbler and Lawrence's Warbler are described under one of the parental species. The Red-whiskered Bulbul, the only member of the Pycnonotidae within the range of this book, also occurs only around Miami, yet it has an entire (half-empty) page to itself. If this and the other "exotic" families were to be included in the book, they certainly (perhaps especially) deserved illustration; yet even where there is plenty of room for a photograph, none has been supplied (Pycnonotidae, Timaliidae, Cotingidae, Zosteropidae). It also seems a great shame that when an author has gone to such obvious pains to write in a space-saving style, the composers could not have honored his efforts by adjusting the illustrations and text so as not to leave quite so many half-blank pages.

The photographs are, for the most part, adequate but undistinguished. The Jaçana looks as though it is a mounted specimen, but others (notably passerines at their nests) are quite nice. The printing process, however, is such that the "black and white" illustrations lack crispness, coming out in varying shades of fuzzy gray. They cannot compare with the excellent reproduction quality in Brown and Amadon's "Eagles, Hawks and Falcons of the World" published recently by the same Audubon Society-McGraw-Hill coalition, and selling at a comparable price per volume. The colored photographs are variable, some very poor, but others good. The Black-necked Stilt settling over its eggs with its incubation patch in full view is particularly interesting, but curiously no mention is made of this in the caption or the text. The Cinnamon Teal is dreadful, being apparently of wing-clipped birds, and in garish color. I should have thought that when using only 31 color plates in a book of this price, better photographs could have been selected. Again, in comparison with Brown and Amadon, the present book suffers badly.

In summary, this "handbook" is a compilation of the basic knowledge on North American and Hawaiian birds. Careful attention has been given to accuracy of detail, and therefore it will be a valuable reference book for years to come. It is unfortunately rather dull to read, and has numerous inconsistencies, particularly in balance of treatment between and among species. It is, however, easy to use and should be both comprehensible and useful for the beginning student. Technical terms and jargon have been successfully avoided, and it is adequately indexed. The Handbook seems to have been designed for the bird watcher who wishes to go beyond his Peterson guides, but is not yet ready to invest in a set of Bent's Life Histories or other detailed references. With the low quality of illustration reproduction, however, I question whether it is a bargain for anyone at \$25.

—MARY HEIMERDINGER CLENCI.

HANDBUCH DER VÖGEL MITTELEUROPAS. Volume 1. Gaviiformes—Phoenicopteriformes. By Kurt M. Bauer and Urs N. Glutz von Blotzheim. Edited by Günther Niethammer. Akademische Verlagsgesellschaft, Frankfurt am Main, 1966: 6 × 9¼ in., 483 pp., many bl. and wh. illus., 14 maps. Price not given.

This first book of a proposed eleven-volume series, has grown out of the old German classic, "Handbook of German Ornithology," a three-volume work by Niethammer (1937, 1938, and 1942). The original coverage has been expanded both in terms of geography and content. Now encompassing central Europe, the text has additional headings such as "behavior" and "survey of the population" under each species treated. Completely dropped from the old text is the subject of parasites.

The book is organized in much the same way as Palmer's "Handbook of North American Birds" and this first volume likewise brackets the same taxonomic span: loons through flamingos.

The most obvious shortcoming of this handbook is the paucity of maps. There are only 14 used as aids in summarizing banding returns, distributions and migration routes. Even very small distributional maps as found, for example, in Robbins, et al., "Birds of North America" could have been put to good advantage and saved much verbiage. Even a map of the area covered by this book—i.e., central Europe—would have been most helpful. This area roughly takes in the Netherlands, Belgium, Luxembourg, Germany, Switzerland, Austria, Czechoslovakia, and Hungary.

Another deficiency exists under the heading of vocalizations. The sounds are given in phonetic syllables. The limited value of this method is at once apparent when it is encountered in a language other than one's own. Furthermore, I should think that "quärrärk quärrärk gwo gwo" conveys a limited amount of information even to one who speaks German. This space might better have gone to audiospectrographic representation of the vocalizations.

The sections on behavior are done especially well with generous illustrations. Another valuable feature is the extensive reference material presented both at the beginning of the book and throughout the text. In the introduction is a bibliography of the birds of the world organized by regions, as well as references listed under general avian topics as reproduction, food, migration, etc.

In determining the need for such a book, the authors consulted not only their colleagues but potential laymen users as well, and so they included such items as simplified keys to orders, families, genera, and species.

This concise book is not only an important reference for those interested in European ornithology but it also, at a glance, points out the gaps in our avian *Kenntnis* and thus, as Niethammer observed, this and following volumes will undoubtedly stimulate further research.—SAM E. WEEKS.

ANNOUNCEMENT

The Office of Science and Technology has released a report entitled "Systematic Biology—A Survey of Federal Programs and Needs," obtainable from Superintendent of Documents, Washington, D.C. 20402. Price: \$1.25.

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Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subsequently identified. Summaries of major papers should be brief but quotable. Where fewer than five papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "Style Manual for Biological Journals" (1964. AIBS). Photographs for illustrations should be sharp, have good contrast, and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

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PLAN TO ATTEND THE 1970 ANNUAL MEETING

The 1970 meeting of the Wilson Ornithological Society will be held jointly with the Cooper Ornithological Society at Colorado State University in Fort Collins from Wednesday, 18 June to Sunday, 21 June 1970. The meeting is being sponsored jointly by Colorado State University and the Colorado Field Ornithologists. The chairman of the local committee for arrangements is Dr. Ronald A. Ryder, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80521. The program chairman is Dr. Keith Dixon, Department of Zoology, Utah State University, Logan, Utah 84321. Detailed information concerning accommodations, transportation, and a call for papers will be sent to all members with advanced registration forms. Reasonably priced food and lodging will be available in modern dormitories within a block of the Student Center. Good facilities and activities are planned for families.

Approximately 75 species of birds should be available at this season in the vicinity of Fort Collins. Field trips will be made to nearby Rocky Mountain National Park where one can observe such species as White-tailed Ptarmigan, Brown-capped Rosy Finch, Water Pipit, Clark's Nutcracker, Gray Jay, Steller's Jay, Common Raven, Blue Grouse, Northern Three-toed Woodpecker, and Pygmy Nuthatch. Trips will also be made to the Pawnee Site of the International Biological Program's Grassland Biome Study east of Fort Collins where Mountain Plovers, McCown's and Chestnut-collared Longspurs as well as large numbers of Colorado's state bird, the Lark Bunting nest. Golden Eagles, Prairie Falcons, Ferruginous Hawks, Swainson's Hawks, and Burrowing Owls also nest in the vicinity. White Pelicans, Double-crested Cormorants and various herons can be observed nesting at other locations in northcentral Colorado.

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THE WILSON ORNITHOLOGICAL SOCIETY

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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.

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

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CONTENTS

- THE HABITS AND RELATIONSHIPS OF THE MAGELLANIC WOODPECKER
Lester L. Short 115
- THE POMARINE JAEGER AS A BROWN LEMMING PREDATOR IN NORTHERN
ALASKA *William J. Maher* 130
- A POPULATION ESTIMATE OF THE DUSKY SEASIDE SPARROW .. *Brian Sharp* 158
- AN INVESTIGATION OF TERRITORIAL BEHAVIOR IN THE AMERICAN
REDSTART UTILIZING RECORDED SONGS
Roy A. Ickes and Millicent S. Ficken 167
- THE WINTER TERRITORIES OF TUFTED TITMICE *Ralph W. Condee* 177
- FOOD HABITS AND FEEDING BEHAVIOR OF THE BALTIMORE ORIOLE IN
COSTA RICA *Richard L. Timken* 184
- EN ROUTE BEHAVIOR OF HOMING HERRING GULLS AS DETERMINED BY
RADIO-TRACKING *William E. Southern* 189
- MOLT AND TAXONOMY OF RED-BREASTED NUTHATCHES *Richard C. Banks* 201
- A COMPARATIVE STUDY OF THE FOODS OF THE SORA AND VIRGINIA
RAIL *Gerald J. Horak* 206
- A NEW TURKEY FROM THE PLIOCENE OF NEBRASKA
Larry D. Martin and James Tate, Jr. 214
- GENERAL NOTES
- CONJOINED TWIN DARWIN'S RHIEA *Donald Bruning* 219
- A SWIMMING BALD EAGLE *Theodore R. Merrell, Jr.* 220
- SHARP-TAILED GROUSE GIVES AGGRESSIVE DISPLAY TO AUTOMOBILES
Robert W. Nero 221

RING-BILLED GULL AND LAUGHING GULL CATCH FISH BY "PLOUGHING" AND "SKIMMING"	<i>Karl Eric Tolonen</i>	222
A PUTATIVE SKELETAL SPECIMEN OF THE FLAMMULATED OWL WITH ALABAMA LOCALITY DATA	<i>Glen E. Woolfenden</i>	223
THE DOUBLE-SCRATCH IN THE SEASIDE SPARROW	<i>Frank Enders</i>	225
NEST-BUILDING, INCUBATION PERIOD, AND FLEDGING IN THE BLACK-CHINNED HUMMINGBIRD	<i>Salome Ross Demaree</i>	225
ACTIVITY OF MIGRANT THRUSHES AS DETERMINED BY RADIO-TELEMETRY <i>Charles G. Kjos and William W. Cochran</i>		225
FIRST SPECIMENS OF CHESTNUT-COLLARED LONGSPUR AND LITTLE GULL FROM CONNECTICUT	<i>Walter Bulmer</i>	226
CIRCLE-SOARING BY MIGRATING NIGHTHAWKS	<i>Helmut C. Mueller</i>	227
METHOD OF SEARCHING FOR FOOD BY THE SWAINSON'S WARBLER ..	<i>Brooke Meanley</i>	228
RUFOUS-CROWNED TANAGERS FEEDING ON FRUITBOWL	<i>F. Haverschmidt</i>	228
ORNITHOLOGICAL NEWS		229
ORNITHOLOGICAL LITERATURE		230
Leslie Brown and Dean Amadon, <i>Eagles, Hawks and Falcons of the World</i> , re- viewed by Kenneth C. Parkes; Crawford H. Greenewalt, <i>Bird Song: Acoustics and Physiology</i> and <i>How Birds Sing</i> , reviewed by William W. H. Gunn; C. Clayton Hoff and Marvin L. Riedesel (Eds.), <i>Physiological Systems in Semi- arid Environments</i> , reviewed by J. W. Hudson; Elizabeth S. Austin (Compiler and Editor), <i>Frank M. Chapman in Florida: His Journals and Letters</i> , re- viewed by Eleanor Rice Pettingill; Joe Van Wormer, <i>The World of the Canada Goose</i> , reviewed by James Tate, Jr.		
PUBLICATION NOTES AND NOTICES		239

THE HABITS AND RELATIONSHIPS OF THE MAGELLANIC WOODPECKER

LESTER L. SHORT

THE Andes Mountains from central eastern Chile and central western Argentina south to Tierra del Fuego are cloaked with a south temperate forest dominated by various species of southern beech (genus *Nothofagus*) trees. Such forests are the home of a unique avifauna (Vuilleumier, 1967), including three species of woodpeckers. Only two of the latter actually gain their sustenance in true woodpecker fashion within the confines of the forest. The third species, the Chilean Flicker (*Colaptes pitius*), forages mainly on the ground about the edges of the forest, and around small isolated patches of forest in open country. The two forest woodpeckers are the small Striped Woodpecker (*Dendrocopos lignarius*) and the large Magellanic Woodpecker (*Campephilus magellanicus*). The latter was the subject of brief studies during late November 1967 in the region north of San Martín de los Andes, Neuquén, and at the Río Villegas, 54 km south of San Carlos de Bariloche, Río Negro. My particular interest in this species stemmed from its supposed close relationship (e.g., Peters, 1948) with the North American ivory-billed woodpeckers (*Campephilus principalis* and *C. imperialis*). Vocalizations were recorded on tape, and movies were obtained, mainly of one nesting pair of birds at Río Villegas on 28–29 November.

ECOLOGY AND HABITS

The general appearance of this large woodpecker is shown in Figures 1 to 3 (see also Fig. 7); a description is presented below. Magellanic Woodpeckers occurred mainly in mature, little disturbed southern beech forest and mixed southern beech-cypress (*Cupressus*) forest. They were observed less commonly in cutover forest such as that shown in Figure 4. They were common at one and abundant at the other of the two localities where they were studied and they far outnumbered the uncommon *Dendrocopos lignarius*. Northeast of Lake Lolog, 18 km north of San Martín de los Andes, we located at least 13 pairs of these birds within a forest-edge strip about 100 m wide by about 2 km long (Figs. 5, 6).

The sounds of their workings were not very loud; indeed, I could not distinguish with certainty the sounds made by feeding Magellanic Woodpeckers from those of feeding Striped Woodpeckers. The Magellanic Woodpeckers foraged in all parts of the trees. I saw them cling *Dendrocopos*-like to tiny twigs which seemed too small to support them and they fed as well on the main trunks of large (to 1½ m in diameter at breast height) trees. Two birds



FIG. 1. Male Magellanic Woodpecker at nest cavity 54 kilometers south of San Carlos de Bariloche, Río Negro, near the Río Villegas. (Figs. 1-3 from 16-mm color movies.)



FIG. 2. Female Magellanic Woodpecker at nest cavity; mate of male depicted in Figure 1.



FIG. 3. Same female Magellanic Woodpecker as in Figure 2, shown in silhouette with crest in typical position.

foraged on fallen, rotting logs, and one of these briefly descended to the ground while inspecting the fallen log. It struck me that this species seemed to occupy a broad "woodpecker niche," perhaps correlated with the virtual absence of competition. In its diversity of foraging sites it resembled species of *Dryocopus* (e.g., *pileatus*, *lineatus*) more than other campephiline species.

The dimorphism in bill length between sexes of this species (Table 1) is in accord with the possibly broadened "niche" of *Campephilus magellanicus* in the absence of close competitors. Such sexual dimorphism was discussed by Selander and Giller (1963), who stressed its occurrence on islands inhabited by few or one species of woodpecker. It seems obvious that dimorphism in bill size, presumably correlated with differences in feeding habits between males and females (see, e.g., Kilham, 1965; Selander, 1965, 1966; Ashmole, 1967; and Ligon, 1968), can be expected wherever a species of woodpecker exists in the absence of other woodpeckers. In effect the depauperate Fuegian *Nothofagus* forests are an "insular" situation for the Magellanic Woodpecker, as only the terrestrially feeding *Colaptes pitius* and the diminutive *Dendrocopos lignarius* occur sympatrically. Unfortunately, I have too few observations of feeding Magellanic Woodpeckers to demonstrate a difference in feeding habits between males and females. However, it is

TABLE I
SEXUAL OVERLAP IN MILLIMETERS OF THE EXPOSED CULMEN OF
THREE WOODPECKERS (*CAMPEPHILUS*).

Species	♀ range	♂ range	Sexual overlap in range	Per cent range overlap	Per cent joint non- overlap*	N
<i>C. magellanicus</i>	43.5-54.5	51.8-58.5	2.7	18	90	28
<i>C. principalis</i>	60.5-67.5	63.0-72.9	4.5	36	76	54
<i>C. imperialis</i>	72.5-84.7	78.5-85.5	6.2	48	70	34

* Determined from Coefficient of Difference (Mayr, Linsley and Usinger, 1953:146) obtained for both culmen length and bill length from nostril. C. D. values were below 0.70 in both measurements for the two larger species and were 1.29 (culmen) and 1.40 (bill length from nostril) for *C. magellanicus*. The differences exhibited are thought to be the minimal that can obtain, because adults from all areas and all times of the year were utilized. On a local basis, allowing for possible temporal variation, the differences undoubtedly would be greater.

noteworthy that the several individuals that were observed feeding at the tips of small branchlets were females.

Magellanic Woodpeckers foraging on larger limbs and trunks move easily upward with the tail appressed to the surface of the tree and the legs spread outward. The head is often held quite far out from the surface of the tree (Fig. 3). Examination of movies I have taken clearly shows that all the toes of this woodpecker are normally directed forward and laterally, often well spread apart; the position of the toes varied within these limits from that illustrated in Figure 6 A to that in Figure 6 B by Bock and Miller (1959: 22).

The action of the bill in feeding varies from light taps and probes to heavy blows. I never witnessed a sustained flurry of pecking; rather, pecking was deliberate, only one or few pecks being delivered at a time. A female feeding chickadee-like in the outermost branches of a *Nothofagus* tree, used her bill entirely for probing during 10 minutes of observation. Nevertheless, the bill can be used to deliver powerful blows, and I was surprised at the ease with which one or two strong blows of a male cut a piece of bark from a live tree. Workings of these woodpeckers included areas on trees with several small to large (10 cm) pieces of bark removed, and deeply chiseled holes like those of a Pilcated Woodpecker (*Dryocopus pileatus*).

Foraging took place in both dead and live trees (species of *Nothofagus* and *Cupressus*), and in live and dead branches of living trees. Most trees had dead limbs or even fully dead tops; when viewed from a distance the mountain forest at 18 km northeast of San Martín de los Andes, where Magellanic Woodpeckers were abundant, appeared a peculiar gray-green color due to the dead gray tops of many of the trees (Fig. 5). Some feeding takes place on fallen logs, as mentioned above. The birds progress rather



FIG. 4. Cutover *Nothofagus* forest (lower slopes) and mature forest (upper slopes) above Lake Meliquina, about 25 kilometers south of San Martín de los Andes, Neuquén. Magellanic Woodpeckers occupy mature forest, and, sporadically, patches of cutover forest.

rapidly while feeding, moving often from tree to tree. The wings of these woodpeckers produce a flapping sound as the birds fly from tree to tree. The white in their wings (pattern described below) is also very obvious while they are in flight.

Nesting (and, presumably, roosting) cavities are excavated in partly dead trees, and holes seen were 5–15 m above the ground. About 20 such holes were noted, and one is shown in Figure 6. The holes faced in all directions, and varied greatly in shape from almost circular to very oval or droplet-like. One nesting cavity examined closely (by R. S. Crossin) was $5\frac{1}{3}$ m up in a small, nearly dead *Nothofagus* tree about 32 cm in diameter at nest height. The hole was approximately 12×9 cm in dimensions. The cavity was about 40 cm deep and lined at the bottom with a small amount of sawdust and wood chips. Construction of the cavity was not observed. The cavity was occupied by a lone nestling about three days old. The fact that this nest contained only one young bird is interesting, since the only laying adult female that we collected had laid but one egg and contained no other large ova. Johnson (1967) noted a family of three young birds and a clutch of four eggs of Magellanic Woodpeckers in Chile.



FIG. 5. Edge of mature *Nothofagus* forest northeast of Lake Lolog, 18 kilometers north of San Martín de los Andes, Neuquén. Magellanic Woodpeckers were abundant in this forest (see text). Note the dead tops of many trees on the slopes. Cattle were pastured in the foreground (where scattered bamboo clumps are seen), but not in the forest itself.

TAPPING AND DRUMMING

Sounds produced by the Magellanic Woodpecker's bill against wood are of two general types, tapping associated with feeding, and that serving a signal function. The latter may be the functional equivalent of "drumming" in other woodpeckers (e.g., species of *Dendrocopos*, *Dryocopus*, *Colaptes*, etc.), and is hence designated the "drum-tap."

Tapping associated with feeding is variable in intensity, frequency and duration, depending upon the foraging site and the food being sought. There is no single means of feeding (see above). The sounds produced by a foraging Magellanic Woodpecker range from barely audible scraping noises (like those of a nuthatch, *Sitta*) to loud, repetitive taps. In the former case feeding is by probing; in the latter case, it is by the delivering of hard blows with the bill. I was unable to detect a difference in tapping between foraging individuals of *Dendrocopos lignarius* and those of Magellanic Woodpeckers feeding in smaller branches of trees. In those instances when large (about 10 cm in diameter) pieces of bark were chopped out of a *Nothofagus* tree



FIG. 6. The interior of the mature *Nothofagus* forest shown in Figure 5. Amid the large trees with draped mosses and a bamboo understory is the nest cavity (in pale-barked tree above bamboo, left center) of a pair of Magellanic Woodpeckers.

the birds tapped loudly, and deliberately, usually at one to four blows in a series. The sounds of these blows are easily distinguished from drum-taps by their irregular pattern, lesser resonance, and (usually) lesser intensity.

Drum-taps were heard most frequently from one pair near a nest. These loud, hollow-sounding taps were produced by double or (occasionally) single blows against a tree. They may have been directed at me as an intruder near the nest. The drum-tap may serve in the establishment and maintenance of territories, and perhaps also as a location note for members of a pair. The drum-taps of the Magellanic Woodpecker are like those of *Phloeocastes robustus* (Fig. 9), which I heard in northeastern Argentina. Other species of *Phloeocastes* (*P. melanoleucos*, personal observation; *P. guatemalensis*, Slud, 1964; *P. leucopogon*, Wetmore, 1926), and *Campephilus* (*C. principalis*, Tanner, 1942; probably *C. imperialis*, see Nelson, 1898:221) have very similar drum-taps; indeed, these may characterize all campephiline species.

VOCALIZATIONS

Despite the brief time spent observing Magellanic Woodpeckers, several vocalizations were heard and recorded on tape. Other vocalizations prob-

ably remain to be described, and further study of those which are discussed below is necessary to ascertain their functions.

The vocalization uttered most often by the Magellanic Woodpeckers we observed is a variable, double-noted, harsh call, similar to that of *Phloeocoastes rubricollis* described by Snyder (1966:161) as an "explosive, nasal 'ngkah-ngkah.'" From two to five of these double-noted calls were given in each sequence. I noted variants of this call as follows: *pi-caá*; *wieeer*; *kee-aáh* (softer, less harsh); *kee-árg* (harsher, more drawn out); and *kee-yew* (second note less emphatic). The call was emitted by lone individuals, apparently directed at me or elicited by my presence. It was employed also by males and females comprising groups of three or four birds observed 20-23 November at 18 km north of San Martín de los Andes. Here it appeared to be an agonistic vocalization utilized in encounters, but it may also function as an alarm call. The significance of the variation in this call is unknown, although it presumably is related to the various levels of motivation of birds uttering the call.

Another call heard only from the pair of birds studied extensively can be designated the *toot* call. This is somewhat similar to the *kent* call of *Campephilus principalis* (Tanner, 1942), but it lacks the nasal quality of the latter (interestingly, the entire known vocal repertoire of *C. principalis* is comprised of nasal, trumpet-like notes). Single *toot* notes were heard occasionally from members of the pair as they were feeding. These might function as location notes, but they were also emitted in series of two or three notes, often leading into a burst of *pi-caá* calls, by the adult birds near their nest. In one sequence of calls near the nest the male emitted a series of four *toot* calls, followed by five or six *pi-caá* calls, and these in turn were followed by a drum-tap (see above). These notes may have been directed at me.

I heard these woodpeckers utter only two other types of vocalizations. One of these is a low *peep* call heard only near a nest occupied by a single nestling. While I was not certain that the young bird produced this note, it seems likely. The *peep* calls were interspersed with *pi-caá* calls emitted by one or both adults. This situation may have been the result of my presence; the calling young bird may have been hungry, and the disturbed adults may not have been feeding it a sufficient amount of food. Another call, heard only once, was a loud, prolonged *cray-cra-cra-cra-cra-cra*, given by a lone male clinging to a tree about 70 m from me. The bird flew off shortly after it called. Prolonged calls of this nature function in other woodpeckers (e.g., species of *Dendrocopos* and *Colaptes*; personal observation) in the establishment and defense of territory, but the lone instance of this call in the Magellanic Woodpecker provides no basis for speculation regarding its function.

DATA FROM SPECIMENS

Various data were obtained from 16 specimens that we collected, including one unfeathered nestling and 15 adults. Many of these were prepared as alcoholic specimens and skeletons for anatomical investigations.

The adults examined generally had irides colored pale yellow near the pupil, progressively becoming gold, and finally orange, away from the pupil. One bird had irides uniformly yellow, but with flecks of orange scattered throughout.

Most of the adult specimens, collected from 20–29 November, had not yet commenced breeding. One female (collected on 20 November) had laid an egg; its ovary measured 20×10 mm, and a brood patch was present. Six other females had ovary measurements of from 8×5 mm to 15×11 mm. One of the latter had slightly enlarged ova (to 2 mm) and an incipient brood patch, another had a defeathering brood patch, and a third female showed slight enlargement of the oviduct. The single nestling was obtained on 29 November.

Weights of seven adult males ranged from 312 to 363 g, with an average of 338.4 g. Six females weighed from 276 to 312 g, averaging 291.3 g. A female laying eggs weighed 326 g.

A brood patch was evident in only three of seven males that were collected, including the mate of the female that had laid an egg. These brood patches were not completely formed. The testes of six of these males measured from 4×2 mm to 10×8 mm.

The sole nestling was prepared as an alcoholic specimen, and few data are available for it. The essentially featherless, two or three day old bird was alone in a nest cavity (described above); its weight was 29.6 g.

A COMPARISON OF THE EXTERNAL MORPHOLOGY OF THE
MAGELLANIC WOODPECKER WITH OTHER CAMPEPHILINE WOODPECKERS

The Magellanic Woodpecker is a large picid exceeded in size among the woodpeckers only by several species of the genera *Campephilus*, *Dryocopus*, and *Mulleripicus*. Like the other campephiline woodpeckers this species has a (moderately) broad bill, and the inner two pairs of its rectrices are especially hard and stiff. Among the campephiline woodpeckers the Magellanic Woodpecker is usually considered a close relative of the North American ivory-billed woodpeckers (*Campephilus principalis* and *C. imperialis*, which probably comprise a superspecies; see Fig. 7). It approaches them in size, and in its white wing patches, which are visible when the bird is perched; the curled crest of the female is also like that of the female of *C. imperialis*. However, there are numerous differences between the Magellanic Woodpecker and the northern ivory-bills.



FIG. 7. From left to right are adult pairs of Magellanic Woodpecker (*Campephilus magellanicus*), Imperial Woodpecker (*C. imperialis*) and Ivory-billed Woodpecker (*C. principalis*). The male of each species is at the left, and the female at the right.

The Magellanic Woodpecker has a large white wing patch restricted to the inner web of the secondaries and the basal portion of the inner vane of the primaries; the primaries are never tipped with white. In contrast, the northern ivory-bills have white over the entire distal portion of all secondaries, and white progressively restricted from the inner to the outer primaries toward their tips and not their bases. This renders the flight pattern of these birds entirely different. Like *Phloeocoastes guatemalensis* and *P. melanoleucos* (see Figs. 8, 9) and the Pileated Woodpecker (*Dryocopus pileatus*), the Magellanic Woodpecker exhibits a *single*, anterior, white underwing patch, because the white in its flight feathers is continuous with that of the underwing coverts. The northern ivory-bills exhibit *two* white wing patches, an anterior patch formed by the white coverts, and a posterior white patch separated from it by the black bases of the flight feathers (see Tanner, 1942:2).

The Magellanic Woodpecker has relatively narrow, tapered outer (tenth) primaries, but the northern ivory-bills have even narrower, strongly falcate outer primaries. The rectrices of the Magellanic Woodpecker are less sturdy than are those of its northern relatives, and the second rectrices often exhibit so much wear that the central rectrices stand apart from them; these two



FIG. 8. From left to right are a male *Campephilus* (*Phloeoceastes*—see text) *guatemalensis*, a female of that species, a female Magellanic Woodpecker, and a male and female of *Campephilus leucopogon*.

pairs of rectrices are equal in the northern ivory-bills. The bill of the Magellanic Woodpecker is black, never ivory in color like the bills of *C. imperialis* and *C. principalis*, which are also relatively sturdier, more massive and broader (more wedge-shaped from a dorsal view) than that of *C. magellanicus*. Indeed, the bill of the Magellanic Woodpecker is proportionally less massive than that of several species of *Phloeoceastes* (especially *P. leucopogon*, Fig. 8). This is particularly reflected in the weak ridge on the gonyes of *Campephilus magellanicus*, as compared with *C. imperialis*, *C. principalis*, *Phloeoceastes leucopogon*, *P. melanoleucos*, and *P. robustus*. The bill size difference between the sexes of *C. magellanicus* was discussed above; this difference is greater than that occurring between the sexes of *C. principalis* and *C. imperialis*.

The male Magellanic Woodpecker has an all-red head and a rather short crest, matched among campephiline woodpeckers by *Phloeoceastes guatemalensis*. The female typically has a long, curled crest resembling that of the female of *C. imperialis*. Some species of *Phloeoceastes* such as *P. leucopogon*, *P. melanoleucos* and *P. guatemalensis*, have males with essentially all-red



FIG. 9. From left to right are a female and a male of *Campephilus melanoleucus*, a female Magellanic Woodpecker, and a male and female of *Campephilus robustus*.

heads, including the crest, and females with a crest that is black anteriorly and red posteriorly. The black crest feathers of these females are usually more elongate than the red feathers (sometimes red feathers are longer, but, if so, they have black tips). These black crest feathers occasionally curl somewhat forward (specimens of *P. leucopogon* and *P. melanoleucos*). I suggest that differential wear of black and red feathers may have been a factor in the evolution of the crests of these species, for melanin-containing feathers appear to be more durable and resistant to wear than are red feathers. The evolution of the three large species of *Campephilus* has been marked by reduction or elimination of red in the female's crest and head pattern. In the northern ivory-bills the females have entirely lost their red coloration of the head, and their long crests are black. The males of these two species have a reduced amount of red in the crest; essentially they have assumed the *female* head pattern of *Phloeoceastes melanoleucos* and *P. guatemalensis*. However, males of the northern ivory-bills have the red feathers of the crest longer than the black ones. The head pattern of the Magellanic Woodpecker has developed differently. The female of this species has a reduced amount of red, which occurs around the bill (the only other campephiline species the

females of which have red in this region is *Phloeoceastes guatemalensis*), and a curled black crest. However, reduction of red coloration has not occurred in the male. Instead, the latter has an all-red head like that of *Phloeoceastes guatemalensis* and *P. leucopogon* (the latter has a longer crest, however).

The Magellanic Woodpecker resembles *Phloeoceastes rubricollis* and differs from all other campephiline species in the absence of white on its back and neck. Ventrally, most specimens show some evidence of white at the tips of the abdominal feathers. A few individuals have most abdominal feathers with white tips. This condition gives a somewhat barred appearance to the abdomen, perhaps reflecting such a pattern in the ancestors of *C. magellanicus*. No other campephiline species with black underparts (*C. imperialis*, *C. principalis*, *Phloeoceastes leucopogon*) exhibits this white barring.

COMMENTS ON RELATIONSHIPS OF CAMPEPHILINE WOODPECKERS

The Magellanic Woodpecker has been considered to comprise a monotypic genus (*Ipocrantor* Cabanis and Heine), or to be congeneric (in *Campephilus* Gray) with the northern Imperial and Ivory-billed Woodpeckers. I believe that the Magellanic Woodpecker is not related directly to the northern ivory-bills, but rather is related to them indirectly by virtue of the independent evolution of both groups from species of *Phloeoceastes* Cabanis. The similarities between the Magellanic Woodpecker and the northern ivory-bills (e.g., tendency toward a falcate outer primary, longer gonys, plumage patterns; see above) seem to be the result of parallel evolution of large woodpeckers from the same basic ancestral stock of *Phloeoceastes*. Other similarities among the three large "ivory-bills" (e.g., vocalizations, color pattern, tail structure; see above) are shared with various species of *Phloeoceastes*. On the other hand the differences (see above) between the Magellanic Woodpecker and the northern ivory-billed group appear to reflect their recent independent evolutionary history.

The "generic" characters setting *Campephilus* and *Ipocrantor* apart from *Phloeoceastes* (chiefly their more falcate primaries and longer gonys, *Ipocrantor* being intermediate in the latter respect between *Campephilus* and *Phloeoceastes*; see Ridgway, 1914:9-10) are trivial and possibly correlated with the larger size of these birds. In any event, species groups within *Phloeoceastes* (these groups are: the *P. leucopogon-guatemalensis-melanoleucos-guayaquilensis* group; the *P. robustus* group, probably including *P. rubricollis*; and the *P. haematogaster-pollens* group) seem at least equally as distinct as *Campephilus* and *Ipocrantor*. The recognition of the latter two genera seems to necessitate the splitting apart from *Phloeoceastes* of at least two genera ("*Cniparchus*," "*Scapanens*"; for their characters see Ridgway, 1914) for taxonomic consistency.

The various groups of campephiline species, including the Magellanic Woodpecker group and the northern ivory-bill group, can be accommodated within a single genus (*Campephilus*) comprised of 11 species. These species are so fundamentally similar in coloration, structure and habits that their inclusion in one genus far better expresses their relationships than does splitting them into two genera (*Campephilus* and *Phloeoceastes*; this would be incorrect, as the species of *Campephilus* are not strictly monophyletic), three genera (*Campephilus*, *Ipocrantor*, and *Phloeoceastes*), five genera (the three last mentioned, *Cniparchus* and *Scapanus*) or even more genera (e.g., including *Megapicos* Malherbe). Hence, I follow Bock (1963) in considering the campephiline woodpeckers to comprise the single genus *Campephilus*.

SUMMARY

The large Magellanic Woodpecker (*Campephilus magellanicus*) inhabits the *Nothofagus* forests of southern South America, where only one small species of woodpecker (*Dendrocopos lignarius*) is a sympatric potential competitor. In the virtual absence of competition the Magellanic Woodpecker forages in diverse ways and at various sites. The sexes differ in bill length (almost no overlap between sexes), probably correlated with a difference in feeding habits. Nesting sites vary, as may the size of the clutch. The breeding season in southwestern Argentina commences in November. Drum-tapping is generally like that of other campephiline species for which data are available. Vocalizations resemble those of the Ivory-billed Woodpecker (*Campephilus principalis*) and other campephiline species (e.g., *Phloeoceastes rubricollis*). The Magellanic Woodpecker shows certain morphological similarities with the northern ivory-billed species (*Campephilus principalis* and *C. imperialis*), but also many differences which suggest that these two groups of woodpeckers independently evolved from ancestral species of *Phloeoceastes*. It is suggested that the Magellanic Woodpecker and the northern ivory-bills comprise but two of five groups of campephiline woodpeckers, no group of which is sufficiently distinct to merit separate generic recognition. Accordingly, the 11 species of campephiline woodpeckers are considered congeneric (genus *Campephilus*).

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THE POMARINE JAEGER AS A BROWN LEMMING PREDATOR IN NORTHERN ALASKA

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THE population fluctuations of many arctic predators, both avian and mammalian, are associated with changes in the numbers of their major prey, the several species of arctic lemmings.

Pitelka, Tomich, and Treichel (1955a) reported that the breeding densities of avian predators near Barrow, Alaska from 1951 to 1953 were correlated with lemming abundance. Their work confirmed that the Pomarine Jaeger (*Stercorarius pomarinus*) is a major lemming predator in northern Alaska and documented qualitatively the relationship of this species with the population cycle of the brown lemming (*Lemmus trimucronatus*) in that region. They also pointed out the desirability of quantifying the relationship between the two species. Accordingly the major objective of my study was an attempt to define the relationship between the populations of the Pomarine Jaeger and the brown lemming quantitatively, in order to determine the role of avian predators in the lemming cycle. In this paper I will discuss the food habits, nesting density, and reproductive success of the jaeger population and try to assess the impact of their predation on the brown lemming population. The interactions of populations in a simple system involving a single prey species and several avian predators should contribute to understanding of predator-prey relationships in general, in addition to the specific question of the role of predation as a possible cause of the lemming cycle itself.

My study was conducted for five seasons in northern Alaska through a complete lemming cycle, beginning with a high lemming population in 1956 and terminating with a second lemming high in 1960. Most of the field work was done at Barrow, although data were also obtained at Pitt Point, Wainwright, and Cape Sabine (Fig. 1). Additional observations were made in 1954 and 1955 when I was employed at Barrow by the U. S. Geological Survey. I was at Barrow briefly in the summer of 1953 and witnessed the lemming high of that year.

ENVIRONMENT

Barrow is at the northern tip of Alaska at approximately 70°N. Latitude. It is at the apex of a wide triangular coastal plain that is 400 miles from east to west and 80 miles from north to south at its widest longitude through Barrow (Fig. 1).

This paper is concerned with the portion of the coastal plain within which the brown lemming population cycles regularly, as well as with a coastal strip

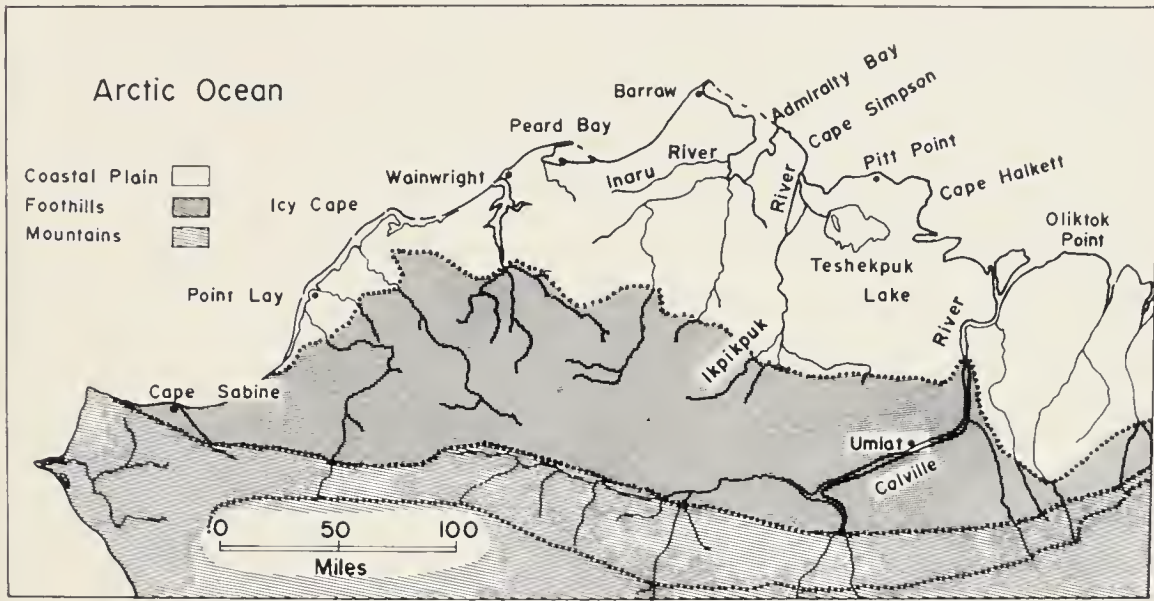


FIG. 1. Map of northern Alaska with place names mentioned in the text.

usually less than five mile wide, extending from Cape Sabine on the West to Oliktok Point on the east, within which the brown lemming population fluctuates irregularly. The portion of the coastal plain within which lemming highs regularly occur is triangular and extends 80 miles east and west of Barrow and 25 to 30 miles inland at its widest point south of Barrow. The environmental description applies to the area thus defined.

The northern part of the north Alaskan coastal plain is a region of low relief, extensive marshy areas, meandering streams, and numerous lakes and ponds. The development of mature drainage has been impeded by the level topography and by underlying permafrost. Twenty per cent of the area is covered by lakes (Spetzman, 1959) and more than 50 per cent is covered with standing water (Black and Barksdale, 1949).

The vegetation of this region, as of tundra generally, is low. The vegetation on mesic and wet sites at the end of the growing season averages approximately six inches in height. The vegetation on dry sites is lower, and on a few favourable wet sites it can be several inches taller.

Marsh areas dominated by *Carex* species, especially *Carex aquatilis*, cover approximately one-third of the land area under consideration (Thompson, 1955b). Marsh usually occurs on a saturated peat substrate, often with one to three inches of standing water. Marsh vegetation occupies the saucer-like depressions of low-center polygons (Thompson, op. cit.) as well as extensive marshes in partly drained lake basins and around the edges of ponds and lakes. Elevated drier sites typically contain a poorly developed tussock-heath tundra association (Britton, 1957 and Spetzman, 1959). This association is

essentially a simple mat of sedges and grasses with a minor element of prostrate willow shrubs, heath species, mosses and lichens. *Eriophorum vaginatum*, which further inland forms large tussocks, is here reduced in stature and inconspicuous. The most common heath elements are *Ledum groenlandicum*, *Vaccinium vitis-idaea*, and *Cassiope tetragona*.

The climate of the arctic coast of Alaska is severe. Winters last nine to ten months and are cold. Summers are short and cool. The average annual temperature at Barrow is 10.1°F. The mean temperature for February, the coldest month, is -18.1°F, and for July, the warmest month, it is 40.0°F. The mean minimum temperature is above freezing from late June to early August. The tundra is free of snow for the latter part of June, July, August, and early September. Frost is possible in all months. The mean annual precipitation averages 4.1 inches at Barrow. The sun is above the horizon continually for 87 days from 9 May through 4 August.

Cape Sabine is in the northern foothills of the Brooks Range where they reach the coast (Fig. 1). The study area, about one mile inland, is characterized by long parallel rocky ridges separated by broad shallow swales. The vegetation is much more complex than in the portion of the coastal plain described above. Well developed tussock-heath tundra covers the slopes and luxuriant *Carex* marsh occurs in the swales. Marsh vegetation here is dense and is 14 to 16 inches tall by mid-July. The Pomarine Jaegers which bred in the area nested in the swale bottoms.

BACKGROUND

A review of the recent history of the brown lemming population in northern Alaska, and some information on lemming biology and predator biology are necessary for understanding the spatial and temporal aspects of the breeding ecology of the Pomarine Jaeger.

The brown lemming population of northern Alaska has been studied continuously since 1949. Details of population fluctuations and other aspects of lemming ecology are in Rausch (1950), Thompson (1955a, 1955b, 1955c), and Pitelka (1957a and 1957b).

Lemming highs are characteristic of coastal tundra in northern Alaska (Pitelka, 1957a), and seem to be confined to the northern portion of the coastal plain, already described, where, as a result of climatic modification by the arctic ocean, the tundra vegetation is simpler than tundra inland. Two lemming species occur in this area, the brown lemming and the collared lemming (*Dicrostonyx groenlandicus*). The latter species is relatively rare and locally distributed, so that the brown lemming is the only significant microtine rodent in this coastal area.

Up to the termination of this study in 1960 general lemming highs were observed in northern Alaska in 1949, 1953, 1956, and 1960. A general, moderate lemming population occurred in 1952, and low populations occurred in 1950, 1951, 1954, 1955, 1957, 1958, and 1959.

In 1956 maximum lemming density occurred in a triangular area of 1,200 to 1,500 square miles extending south from Barrow 25 miles to the Inaru River, east 60 miles to Cape Simpson, and west 70 miles to Peard Bay. About the periphery of this area was a region of lower population density which was approximately ten miles wide on the western and southern edges but extended 30 miles eastward of Cape Simpson nearly to Pitt Point (Pitelka, 1957a).

In 1960 the western and southern borders of the lemming high were approximately the same as in 1956; but, lemmings were scarce in the area between Admiralty Bay and Cape Simpson and east to the Ikpikpuk River. Eastward from there to Oliktok Point there was a moderately high lemming population occupying a narrow region along the coast. The extent of the 1960 high was also estimated to be 1,200 to 1,500 square miles. Accurate information on the extent of the 1953, and 1949 highs is not available. The evidence suggests that they were confined to the area of the 1956 high.

There were two localized highs of *Lemmus* in northern Alaska in 1957 in areas peripheral to the main area discussed above and out of phase with it. The more extensive of these was centered at Pitt Point approximately 80 miles east of Barrow. Its exact extent was not determined; but it was known to occupy the tundra between Teshekpuk Lake and the Arctic Ocean. Its western boundary was near Longitude $153^{\circ}45' W$. It did not reach the Kogru River (Longitude $152^{\circ}30' W$), but the eastern limits were not determined more precisely. This lemming high occupied an area of 250 to 400 square miles.

A second lemming high occurred in 1957, 90 miles west of Barrow at Wainwright, and extended at least 5 miles inland on the east side of Kuk Inlet. Its extent was not otherwise determined.

The tundra vole (*Microtus oeconomus*) occurs regularly as far north as the northern foothills of the Brooks Range and the southern coastal plain. In that area its population fluctuations are apparently restricted, but occasional local population highs are known to occur. A coastal population of this species co-existing with four other microtine rodents was studied at Cape Sabine from 1957 to 1959 (Childs, 1959). The *Microtus* population built up rapidly in the summer of 1958 and reached a high level at the end of that season. In the summer of 1959 the *Microtus* population was still high, and four pairs of Pomarine Jaegers bred there for the first time. The extent of this high is not known, but it appeared to be local and probably occupied less than 25 square miles.

To summarize: In northern Alaska in 12 seasons from 1949 to 1960 widespread lemming highs occurred four times, a widespread moderate lemming population once, and the lemming population was low in seven seasons. In 1957 there were two local highs at Pitt Point and Wainwright.

The interval between the general lemming highs since 1949 has been three to four years. The amplitude of the fluctuations is large, but lemming density varies between peak years, and estimates of the magnitude of the fluctuation differ greatly. Thompson (1955*b*) estimated that there was a 400-fold increase from the low of 1950 to the 1953 peak at Barrow. Krebs (1964) estimated a 25- to 50-fold increase in the winter preceding the 1960 lemming high at Baker Lake, N.W.T., and a two- to three-fold increase during that summer, following a brief decline at melt-off in June. Shelford (1943) estimated an increase of 800- to 1,000-fold in the lemming cycle at Churchill, Manitoba.

Predators are not evident for two years following a decline from a high. Moderate numbers of lemmings are present either early or late in the third summer of a four-year cycle, and avian predators may exploit the third-year population if lemming density is high enough in the spring.

Although lemmings, like other microtines, sometimes breed in the winter, at Barrow when the snow cover melts in June the lemming population consists mostly of nonbreeding adult animals. Synchronous breeding in the population begins immediately and a large summer generation of lemmings emerges in mid-July. Breeding continues through the summer, and the first summer litter may produce a second generation in August or September. For additional information on the biology of the brown lemming in northern Alaska, the reader is referred to the papers of Rausch, Thompson, and Pitelka cited previously.

Five species of avian predators may be associated with the lemming high. They are the Pomarine Jaeger, the Snowy Owl (*Nyctea scandiaca*), the Parasitic Jaeger (*Stercorarius parasiticus*), the Short-eared Owl (*Asio flammeus*), and the Glaucous Gull (*Larus hyperboreus*). Significant mammalian predators are the least weasel (*Mustela rixosa*) and the arctic fox (*Alopex lagopus*). This study was concerned with the Pomarine Jaeger, but an attempt will be made to assess the total predation impact on the lemming population.

The breeding biology of the Pomarine Jaeger, in northern Alaska has been summarized by Pitelka, Tomich, and Treichel (1955*b*). The Pomarine Jaeger is a moderately large predator on its nesting grounds. Females collected in northern Alaska average 745 grams in weight and males 648 grams. Pomarine Jaegers arrive on the tundra in late May and early June. In breeding years they establish large all-purpose territories. The normal clutch of two eggs is laid in an unlined scrape on the tundra in mid- to late June. The chicks emerge

in mid-July and begin to fly in the last half of August. Adults and young depart in late August or early September.

GENERAL METHODS

Breeding jaegers are easily watched and censused because they are both conspicuous and aggressive and because tundra vegetation offers negligible interference with observation. At Barrow the study area was systematically traversed using a tracked vehicle, a wcaasel. Nests were staked, and the location of nests and territorial pairs was plotted on an outline map traced from aerial photographs. By continually rechecking the location of nests in relation to neighboring nests and landmarks, considerable accuracy was eventually obtained in maps of nest distribution. In 1956 and 1960 the nests on part of the study area were mapped with an alidade and plane-table. Censuses were repeated regularly in the season to determine population trends and breeding success. In areas away from Barrow censusing was done on foot, and pair and nest locations were marked on aerial photographs carried in the field.

The area censused differed between years depending on jaeger density. Thus, at Barrow in years of maximum jaeger density the study area was 5.75 and 6 square miles, while in years of low jaeger density about 15 square miles were censused. The size of the area studied is given with data on breeding density.

For feeding and growth studies nests were encircled with a fence 30 feet long and 12 inches high making an enclosure about 9 feet in diameter. Nine nests were enclosed at Barrow in 1956, one in 1959, and 15 in 1960. One nest was enclosed at Cape Sabine in 1959. When nests were fenced during the incubation period the adults returned to the eggs in minutes and fed the chicks normally when they hatched. Chicks fenced after hatching usually died because the adults did not feed them properly. As jaeger chicks cannot jump, they were not able to escape from the enclosure until they could fly. The enclosed nests were visited at regular intervals, the chicks weighed with a beam balance, and regurgitated pellets and other food remains collected.

Regurgitated food remains were softened in detergent and water. Jaws, skulls, femurs, and pelvises of small mammals, all identifiable remains of birds, and all other food items were picked out. The residue was floated in water so that insect fragments and other small remains were recovered.

The method of analysing the food remains depended on their condition. When pellets were intact, food items were recorded as the percentage of occurrence in the total number of pellets. When regurgitated food material was trampled or picked apart by the jaegers and individual pellets were not recognizable, food items were analysed as the occurrence in the total number of prey items. The number of lemmings and other vertebrate prey was the number of the most numerous bone element, usually the right or left jaw of lemmings. Only the occurrence of food items such as insect remains and egg-shell fragments was recorded for each sample.

Sex ratios of the pelvises removed from all pellets were determined. Separation of male and female pelvises more than 20 mm along the ilium-ischium axis on the basis of their shape is readily done on museum specimens (Dunnire, 1955). However, the most obvious difference between the male and female pelvis is the backward extension of the pubis of the female which gives the posterior border of the pelvis a sloping contour rather than the rounded contour of the male. This part of the female pelvis is thin and mechanical action of digestion often breaks off the pubo-ischial corner, causing the specimen to resemble a male pelvis.

The following criteria were used in addition to shape to distinguish the sexes. All pelves with a least pubic width of 0.7 mm or less were considered female, and all with a least pubic width of 1.00 mm or more were considered male. This separation, based on the results of measuring pelves of 50 males and 50 female museum specimens, can be done with 2 per cent error. The 24 per cent of the pelves with least widths of 0.8 and 0.9 mm were classified on morphological grounds, or rejected if a comfortable decision could not be made.

Two Pomarine Jaeger chicks were raised from hatching at the laboratory in 1960. Two partly grown chicks brought in from the tundra gave additional data on food consumption.

The chicks were placed outdoors in a large cage, eight by eight feet by ten feet high at the age of eight and nine days. Hence they were exposed to natural ambient temperatures, and had much freedom of activity. Records were kept of their daily weight and food consumption.

Systematic observations were made on frequency of feeding of breeding adults.

In 1957 and 1958, nonbreeding jaegers along the ocean near Barrow and Wainwright were collected by Eskimos. The specimens were frozen at the Arctic Research Laboratory, and processed at the end of the season for data on stomach contents, weight and reproductive condition.

Further details on methods will be given where they are appropriate.

RESULTS

Food habits of the jaeger.—The Pomarine Jaeger utilizes a large variety of food on its breeding grounds, although most items occur rarely in its diet, and there are few foods which it obtains in quantity. The very specialized adaptations of the Pomarine Jaeger as a predator are apparent when a distinction is made between the ability of the bird to obtain enough food for survival in nonbreeding years and its ability to feed itself and also raise a brood of chicks.

Nonbreeding populations of Pomarine Jaegers were sampled at Barrow and Wainwright in the low lemming years of 1957 and 1958. The variety of food items in the sample of 56 stomachs (Table 1) suggests that this jaeger is largely opportunistic in its food gathering and takes anything available.

Microtine rodents occurred in 41 per cent (23) of the stomachs, and birds were in 25 per cent (14) of them. Four of five shorebirds were Red Phalaropes (*Phalaropus fulicarius*) and one was a calidrine sandpiper, either *Erolia melanotos* or *E. alpina*. Remains of large birds were mostly unidentified, but included one ptarmigan. Two of 11 bird eggs were Red Phalarope. Carrion included caribou (*Rangifer tarandus*) and one seal (*Phoca* sp.). Marine invertebrates were unidentified squid, polychaete worms, and unidentifiable remains.

It appears from this analysis that jaegers were foraging over the tundra, along the ocean shore, and in the native villages. Caribou and seal remains were probably found near the villages. The marine invertebrates were prob-

TABLE 1
 FOOD OF NONBREEDING POMARINE JAEGERS, 1957 AND 1958

Food items	Number of stomachs	Per cent occurrence
Microtine rodent	23	41
Avian	14	25
Carrion	8	14
Bird egg	11	20
Insect	5	9
incidental in stomach	3	5
predominant in stomach	2	3
Fish	7	12
Marine invertebrate	2	3
Number of stomachs	56	

ably picked up on the beach as I have never observed jaegers robbing other birds of their food near Barrow and Wainwright, as has been frequently described by observers in temperate areas (see Bent, 1921). The only locality at which I did observe this behavior in northern Alaska was at Cape Sabine where there were a large number of Black-legged Kittiwakes (*Rissa tridactyla*); and even there it was uncommon.

Breeding populations were sampled by analysing regurgitated pellets collected on the tundra at Barrow in 1956, 1959, 1960, and at Pitt Point in 1957. Pellets were also collected from chick enclosures at Barrow in 1956, 1959, and 1960, and at Cape Sabine in 1959. Pellets of the current season were distinguished by dried mucus on their surface.

Two of these five jaeger populations were of maximum density (Barrow, 1956 and 1960), one was moderately dense (Pitt Point, 1957), and two were very sparse (Barrow and Cape Sabine 1959). Microtine rodents make up the bulk of the food utilized by all of these populations regardless of their breeding density (Table 2). At Barrow and Pitt Point *Lemmus* is the predominant microtine, *Dicrostonyx* occurs very rarely. *Microtus oeconomus* was the exclusive microtine prey at Cape Sabine.

Food other than microtine rodents is more than 10 per cent of the prey items only in the two sparse 1959 populations, in which it was 17 per cent at Barrow and 12 per cent at Cape Sabine. Birds were the most important prey category after microtine rodents. Bird remains consisted mostly of shorebirds, predominantly chicks, and a few ducklings and passerine birds. Remains of

TABLE 2
FOOD OF BREEDING POMARINE JAEGER POPULATIONS

Food item	Barrow		Pitt Point	Barrow	Capc Sabine
	1956	1960	1957	1959	1959
Total microtine	98.6 ^a	97.8 ^b	100 ^a	100 ^a (83) ^b	88 ^b
Other food	8.5	2.2	3	27 (17)	12
Bird	0.9	1.9	1	9 (7)	12
Bird egg	1.2	3	2	12 (10)	
Fish	0.2	0.3		3 (3) ^a	5 ^c
Insect (incidental)	6.2	1 ^c		3 (3) ^a	2 ^c
Number	432	2500	206	75 (89)	68

^a Per cent occurrence of food item in pellets.

^b Per cent occurrence of food item in total number of food items.

^c Number of occurrences in pellet samples; not included in total of prey items.

large birds, such as ducks, occurred very rarely. Fish and insects are unimportant and carrion, absent.

It seems justified to compare these results with the data from nonbreeding jaeger populations even though they are based on food remains in regurgitated pellets and the latter sample is based on analysis of stomach contents. All prey items found in stomachs were identified by undigestible parts such as feathers and bone, and all (except marine invertebrates) have also been found in pellets. Furthermore, items such as insect fragments, insect eggs and otoliths are readily found in pellets when they are examined thoroughly (see methods).

Nonbreeding populations utilized a much smaller proportion of microtine rodents and a larger proportion of birds than breeding populations did, and carrion and fish were significant components of their diet. Insects were most of the contents of three per cent of the stomachs, whereas they were always incidental in pellets of breeding populations.

These results confirm the great importance of lemmings in the diet of breeding jaegers. The relatively low number of prey items other than lemmings, also suggests that breeding jaegers are dependent on lemmings (or other microtine rodents) for sufficient food for successful breeding. The food habits of nonbreeding jaeger populations confirm this conclusion. Lemmings are the most important prey these birds obtain on the tundra; yet the importance of carrion and fish in their diet suggests that they foraged along the coast because they could not obtain sufficient prey from the tundra to survive or attempt to breed.

Jaeger breeding density and lemming density.—The fact that the Pomarine Jaeger is dependent on the lemming population for food poses problems of

adjustment of the jaeger population to a variable food supply. In order to maintain itself the jaeger population must exploit lemming populations efficiently when they are at densities high enough to support the predator's reproductive efforts. In any area, food will be adequate for jaegers in only one in three, or at best two in four years.

The Pomarine Jaeger responds to the lemming cycle by adjusting the fraction of its population which breeds. This adjustment is locally manifested by fluctuation of the jaeger's breeding density. The species cannot alter its clutch size in response to food supply as do many raptors, including the other major avian lemming predator, the Snowy Owl. Quantitative data on the total Pomarine Jaeger population are not available, but I would like to discuss breeding density changes and reproductive success in relation to lemming numbers.

The estimated density of *Lemmus* at the time of the snow melt-off is used to compare lemming densities between years, because this is a convenient, identifiable point at which to compare lemming populations, and because the jaegers are presumably responding to this initial number of lemmings when they begin breeding activities. The density estimates were made by Pitelka (Barrow) and myself (Barrow and Pitt Point) and are estimates with undetermined margins of error. The order of magnitude indicated by the difference between years is certainly a correct one (Table 3).

Information on changes in nesting density and breeding success of Pomarine Jaeger populations was obtained at Barrow from 1954 to 1960, from Wainwright and Pitt Point from 1956 to 1960, and Cape Sabine from 1957 to 1960. Spring lemming density estimates are only available from Barrow for all years and from Pitt Point in 1957. Information on jaeger breeding density and success in 1952 and 1953 are from Pitelka, Tomich, and Treichel (1955a).

In the nine seasons from 1952 to 1960 at Barrow the Pomarine Jaeger did not breed in three (1954, 1957, and 1958), small numbers bred in two seasons (1955 and 1959) and significant numbers of Pomarine Jaegers nested in only four of the nine seasons (1952, 1953, 1956, and 1960) (Table 3).

Other areas show similar variations in the breeding density of the Pomarine Jaeger. At Wainwright breeding occurred in only three of the five years, and breeding density was low each time. Pomarine Jaegers bred in only two of five years at Pitt Point. In 1957 a moderately high density of jaegers nested in response to a local lemming high; and in 1960, when the general lemming high of that year extended eastward past Pitt Point, a low density population of Pomarine Jaegers bred. Pomarine Jaegers bred only once at Cape Sabine from 1957 to 1960, and then only in very low numbers.

Comparison of spring lemming density with Pomarine Jaeger breeding

TABLE 3
BREEDING DENSITIES AND NESTING SUCCESS OF THE POMARINE JAEGER

Locality	Year	Spring <i>Lemmus</i> density (no./acre)	No. of pairs	Census area (square miles)	Density (pairs/ square mile)	Maximum density (pairs/ square mile)	Breeding success (per cent of eggs)
Barrow	1952	15-20	34	9	3.8	5-6 ^a	30-35 ^a
	1953	70-80	128	7	18.3	25-26 ^a	20-25 ^a
	1954	<1	0	—	—	—	—
	1955	1-5	2	15±	0.13	—	0
	1956	40-50	114	6	19.0	22-23	4
	1957	<1	0	—	—	—	—
	1958	≤1	0	—	—	—	—
	1959	1-5	3	15±	0.20	—	0
	1960	70-80	118	5.75	20.5	25	55
Wainwright	1956		3	2±	1-1.5	—	?
	1957		3-4	4	1.0	—	?
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4-5	?	2±	—	?
Pitt Point	1956		0	—	—	—	—
	1957	30-40	61	6	10.1	15	13
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4-5	1-2	—	—	?
Cape Sabine	1957		0	—	—	—	—
	1958		0	—	—	—	—
	1959		4 ^b	11	0.36	1 ^c	13
	1960		0	—	—	—	—

^a Estimates provided by F. A. Pitelka; see Pitelka, Tomich, and Treichel, 1955a.

^b This jaeger population nested in response to a high density of *Microtus oeconomus* for which no density estimate is available.

^c In suitable nesting habitat.

density at Barrow shows a clear correlation between the two (Table 3). The Pomarine Jaeger does not breed at spring lemming densities estimated to be below one per acre. Some breeding takes place at densities of approximately one to five lemmings per acre. Pomarine Jaeger density increases proportionately with lemming density until the mean maximum jaeger density of 18-20 pairs per square mile is reached. Three lemming highs (1953, 1956, and 1960) supported virtually identical mean Pomarine Jaeger densities near Barrow, though the magnitude of the lemming population peaks were different (Table 3, Fig. 2). The leveling of the Pomarine Jaeger's response curve at

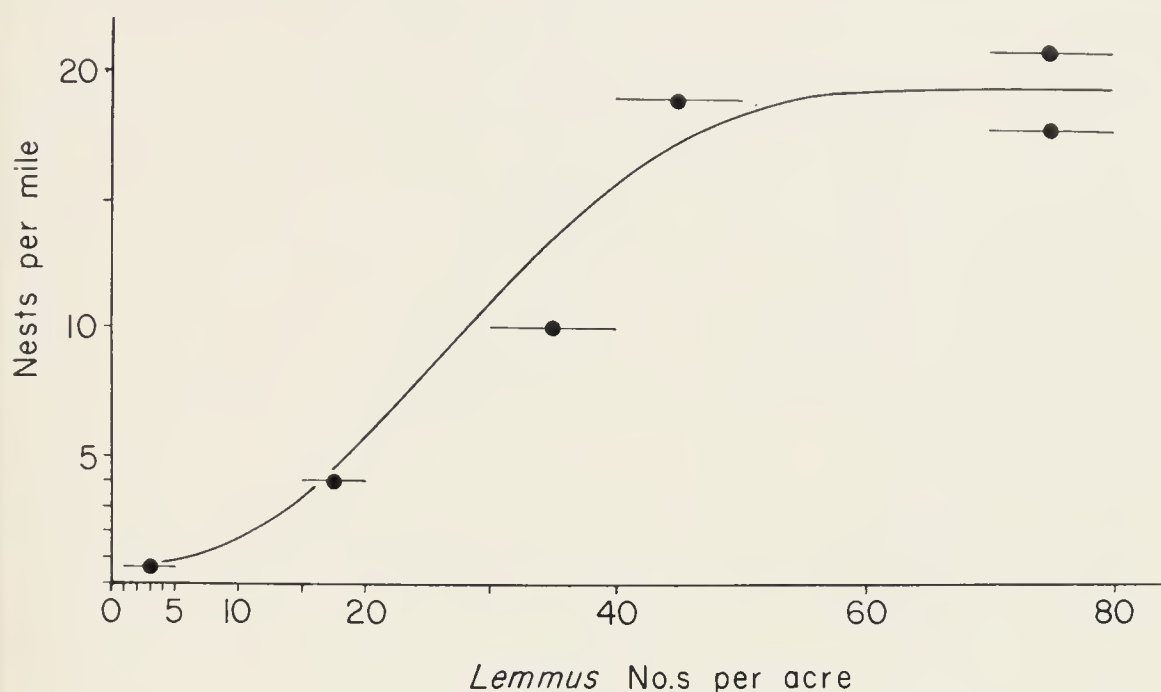


FIG. 2. Relationship between Pomarine Jaeger breeding density and the density of the spring brown lemming population.

high lemming densities suggests that different factors limit the breeding density of jaeger populations at high lemming densities than at low ones. Since the Pomarine Jaeger is strongly territorial and defends an all-purpose territory (Pitelka, Tomich, and Treichel, 1955a), territoriality appears to be the most likely mechanism limiting jaeger density. At jaeger densities below the maximum, food supply is probably limiting, but the question of how food supply acts to adjust Pomarine Jaeger breeding density is unanswered. The response may be related to different thresholds between young adults and more experienced breeders in the population. Fewer of the heavily striped jaegers, which are presumed to be younger individuals, are seen in the sparse breeding populations than are seen in the dense populations.

Breeding success of jaeger populations.—The apparent adjustment of Pomarine Jaeger breeding density to the lemming population level raises the question of the efficiency of the adjustment. The best criterion for judging its efficiency would seem to be the nesting success. If the adjustment of the jaeger's breeding density were efficient at all lemming densities, it should result in a relatively consistent level of reproductive success. In fact, reproductive success has not been constant (Table 3). Breeding success has tended to be low at low nesting densities (Barrow, 1955 and 1959, Cape Sabine, 1959), and low to moderate at intermediate densities (Barrow, 1952 and Pitt Point, 1957). At maximum density, breeding success at Barrow has ranged from

TABLE 4
SIZE CLASSES OF LEMMING FEMURS AND MEAN LEMMING WEIGHTS PER CLASS

No.	Size class (mm)	N	Mean wt. (g)	Weight factor (g)
1	<10	2	8.4	8.0
2	10-15	77	24.8	25.0
3	15-19	8	64.8	65.0
4	>19	22	89.1	90.0

almost complete failure (1956) to moderate success (1953) to high success (1960). The highest breeding success was achieved at high nesting densities.

The maximum populations must contribute most of the recruitment to jaeger numbers, as their large areal extent suggests that they involve a large proportion of the total jaeger population. Yet, breeding success was dramatically different in the two dense jaeger populations at Barrow in 1956 and 1960. Success in those years was clearly related to food supply. In 1956 the lemming population declined during the season (Pitelka, MS) and by late July was not sufficient to sustain the jaegers. Many of the chicks starved and those which did not die of starvation were killed by snow and cold weather on 9 and 10 August. The estimated four per cent success of total eggs laid is generous. In contrast, lemmings remained abundant all through the 1960 season (Pitelka, MS), and chick survival (55 per cent) was the highest recorded.

The sparse breeding populations of the jaeger probably do not contribute significantly to recruitment because of the small fraction of the population which breeds and the low success usually realized. In years when few jaegers breed, nonbreeding jaegers forage on the tundra singly or in large flocks. Breeding failure of jaegers frequently results from interference by these nonbreeding birds, or by nonbreeding Snowy Owls.

These data suggest that the territorial breeding system of the Pomarine Jaeger has evolved to enable the jaeger to limit its exploitation of high populations of lemmings so that the probability of significant reproductive success is increased.

Effect of jaeger predation on the lemming population.—Predators affect the numbers of the prey population directly by the number removed, and indirectly by altering the age and sex structure of the population and, hence, the future course of its dynamics. Four criteria were used to assess the impact of the Pomarine Jaeger on the brown lemming population. They are: (1) the size classes, and hence reproductive status of the removed population; (2) the number of prey taken; (3) the sex ratio of the removed population; and (4)

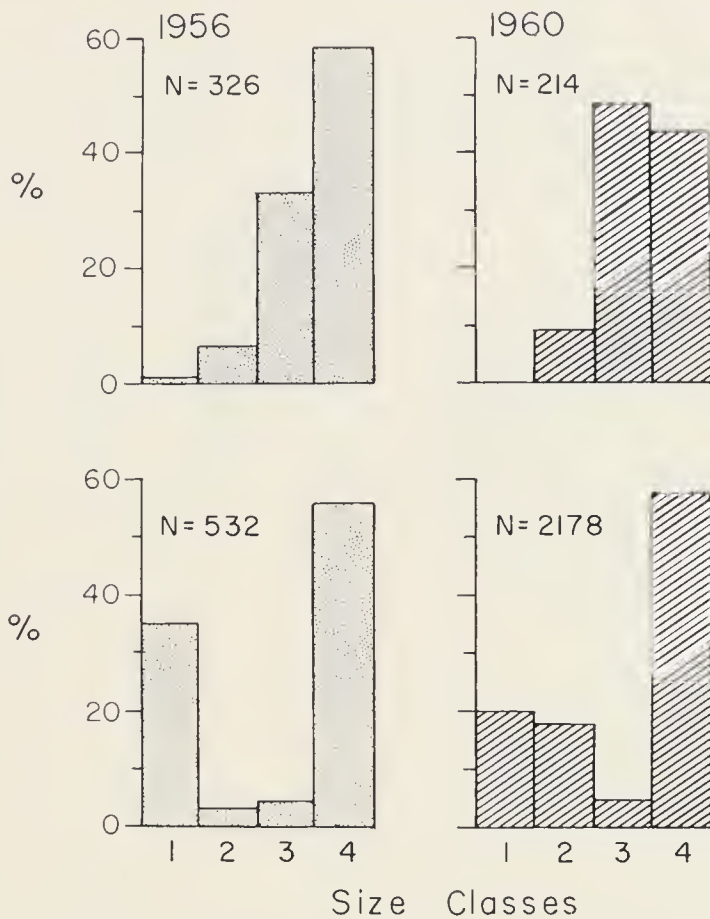


FIG. 3. Size classes of lemming femurs in adult jaeger pellets (top) and penned jaeger chick pellets (bottom) in 1956 and 1960.

the timing of the predator impact in relation to the annual population cycle of the prey.

(1) *Size classes of lemmings taken.*—The impact of jaeger predation on the lemming population can be partly assessed if we know the age groups of the prey affected. Size is used here as an approximate indicator of age and reproductive status. The femurs were sorted into four arbitrary size classes (Table 4). The mean weight of each class was determined from skeletons of animals of known weight (Table 4).

The size classes of lemmings taken early in the season are indicated by the frequency distribution of femurs from adult jaeger pellets from 1956 and 1960 (Fig. 3). Pellets were collected through the season in 1956, but most were collected in late May and June and most collected later were probably from the spring as indicated by the low percentage of the two smallest lemming size classes. The 1960 sample was collected in June. In both seasons most lemmings taken in spring are in classes 3 and 4, which are small and large adult animals.

The size classes of prey taken in the latter part of the season were obtained from chick pellets from enclosed nests. In 1956 chick pellets were collected from 21 July to 9 August and in 1960 from 12 July to 17 August. Large adult lemmings were predominant in both years (Fig. 3). The most significant difference between the two seasons is the occurrence of size classes 1 and 2. The mean weight of the smallest size class is 8.4 g (Table 4).

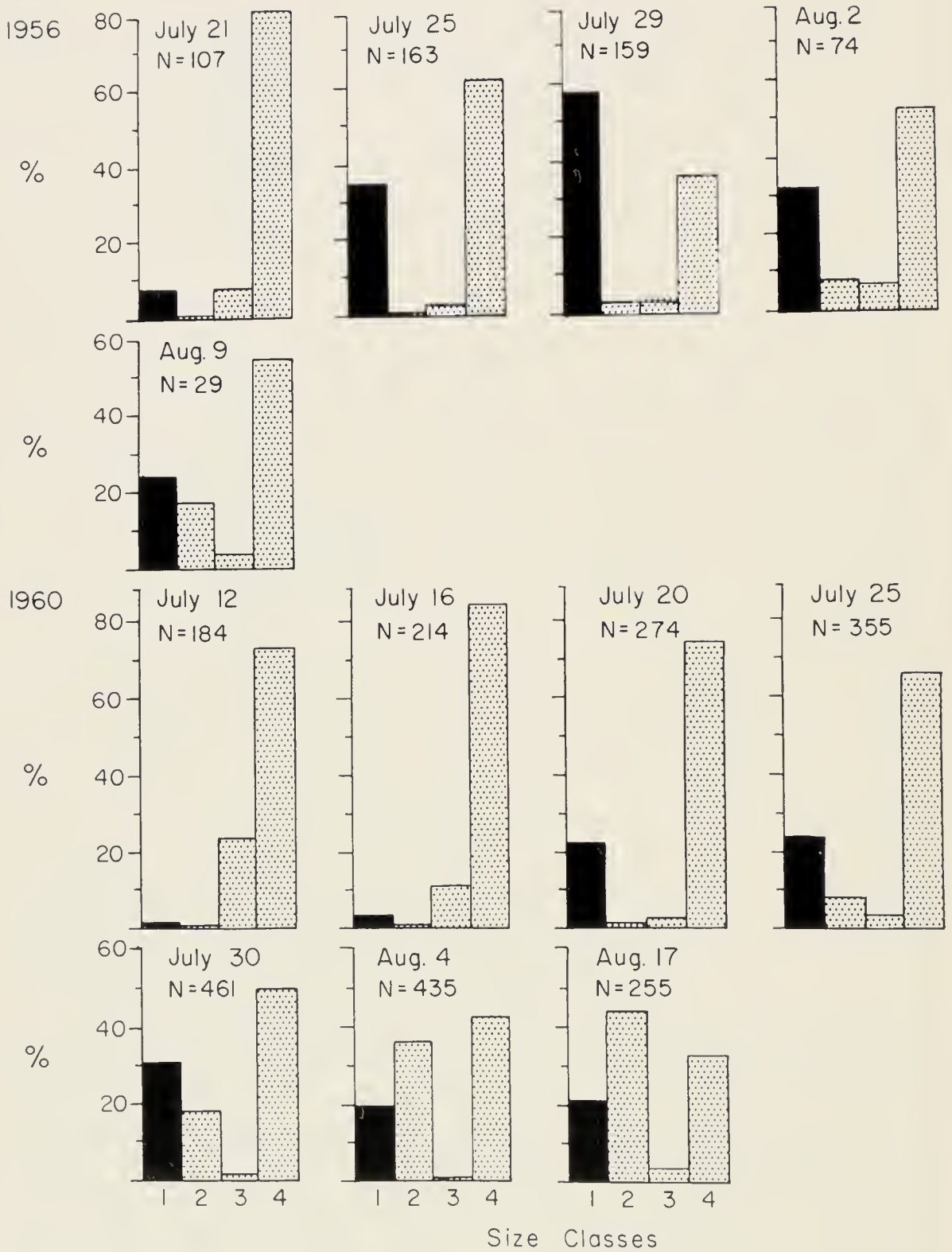


FIG. 4. Size classes of lemming femurs in penne jaeger chick pellets analyzed by short time intervals.

According to Thompson (1955a) young *Lemmus* leave the nest when about 12 g in weight, and are weaned at approximately 15 g. Size class 1 is probably newly weaned lemmings or nestlings. The average weight of size class 2 is about 25 g. In 1956 size class 1 was heavily represented (35 per cent of the total) and size class 2 very slightly represented (3 per cent); whereas in 1960 size class 1 was 20 per cent, and size class 2 was 19 per cent of total lemming prey.

The chick pellets were further analyzed by time intervals to compare seasonal trends in the age classes of prey taken (Fig. 4).

In both seasons adult lemmings were most of the prey in early July. Nestling or newly weaned lemmings, (size class 1) appeared in the jaeger chick pellets in the latter part of July and subsequently increased in importance. In 1956 however, size class 1 formed a far greater percentage of the total than in 1960, 58 per cent on 29 July 1956 vs 31 per cent on 30 July 1960. The difference suggests a comparatively heavy impact on this size class in 1956. Size class 2 appeared in the 1956 sample on 29 July and reached 17 per cent of the total prey by 9 August. In 1960 the same size class appeared in the 25 July sample and steadily increased to 36 per cent of the 4 August sample and 43 per cent of the 17 August sample.

The difference in the prey population in chick pellets in these two years is probably the result of difference in intensity of predation by Pomarine Jaegers in the two seasons. Figures have already been given (Table 3) on the very low reproductive success in 1956 and the very high success in 1960. It is assumed that food shortage and increased hunting intensity in 1956 resulted in a proportionately heavy take of small lemmings as soon as they were available and that the number taken was sufficient to reduce recruitment from size class 1 into size class 2 in that year. In 1960, on the other hand, food was abundant, and there was an ample number of adult lemmings available so that predation on the smaller size classes did not significantly impede recruitment into size class 2.

(2) *The number of prey taken.*—The amount of food eaten by captive chicks is used to estimate food consumption by wild chicks. The use of captive chick food data for this purpose can be justified by comparing the growth rates of the captives with the mean growth rate of penned wild chicks. Growth of Pomarine Jaeger chicks in the first ten days is almost constant. The mean instantaneous relative growth rate of two captive chicks in that period was 16.8 and 15.6 per cent. However, both captive chicks lost weight on their first day and had negative instantaneous relative growth rates from day one to day two. Since eight penned wild chicks had a positive mean instantaneous relative growth rate of 17.5 per cent from day one to day two, I assumed that the weight loss was due to inadequate feeding. If the first days weight loss is ignored the captive chicks had mean instantaneous relative growth rates for the first ten days of 19.5 and 18.0 per cent respectively, approximately the same as the 19.3 per cent for the penned wild chicks in the same age period in 1960 (Fig. 5). Both the weight curve of the successful chick Hotspur and the mean curve of the penned wild chicks leveled off at about 600 g.

The captive chicks were fed mostly on lemming carcasses and a few white mice, thus giving the total number of lemmings as well as the total weight of food eaten (Table 5). Most of the lemmings were entire although some were gutted.

Only one chick (Hotspur, Table 5) was raised from hatching to fledging age. In 47 days this chick ate 9,490 g of *Lemmus* or 202 lemming carcasses. The other chick raised from hatching (MaeDuff) died suddenly when 26 days old. There was no apparent cause of death, the chick began losing weight about 1 August and died three days later. In 26 days it consumed 3,521 g of *Lemmus* and ate 54 lemmings.

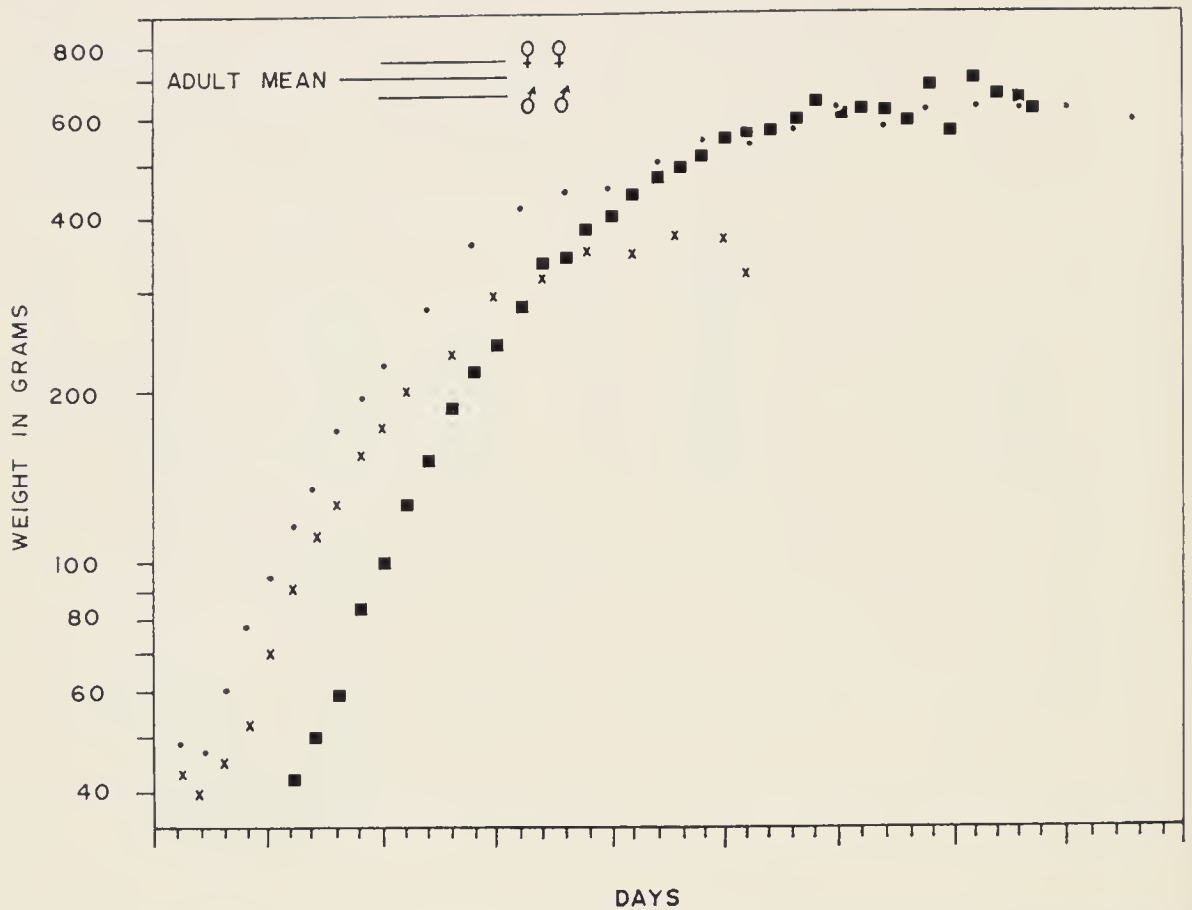


FIG. 5. Weight curves of two laboratory raised jaeger chicks (left) and the mean weight curve of penned jaeger chicks (right).

Two chicks near fledging weight kept for 24 and 28 days consumed an average of about 200 g or 5.5 lemmings per day.

These data suggest that a chick will eat about 9,500 g of food, or approximately 200 lemmings to grow from hatching to fledging. After reaching nearly full size a jaeger chick will eat 200 to 220 g of food per day, or 5.5 lemmings per day.

TABLE 5
AMOUNT OF FOOD CONSUMED BY CAPTIVE POMARINE JAEGER CHICKS IN 1960

Chick	Dates	Age (days)	No. of days	g food	g food/day	No. of Lemmus eaten	Mean no./day
Hotspur	11 July-3 August	1-24	23	3,671	160	54	2.3
	4-27 August	25-48	24	5,819	242	136	5.7
	Total	1-48	47	9,490	202	190	4.0
MacDuff	10 July-4 August	1-26	25	3,521	141	54	2.2
Cathy	4-27 August	??	24	5,105	213	136	5.7
Archy	31 July-27 August	??	28	5,550	198	151	5.4

TABLE 6
NUMBER OF LEMMINGS TAKEN BY POMARINE JAEGER PAIRS IN 24 HOURS

Date	Year	Male	Female	Total
7-8 July	1956	3	1-2	4-5
18-19 June	1960	3	8-9 ^a	11
7-8 July	1960	3.5 ^b	1.5 ^c	5
23-24 July	1960	2	2	4-5 ^d
13-14 August	1960	4 ^e	3	7

^a One lemming was torn apart but apparently only partly eaten.

^b Male caught and gutted two and was seen feeding on another lemming carcass. These were each counted as 0.5 lemming.

^c Female caught and ate part of one, was seen picking at carcasses twice. These were also each counted as 0.5 lemming.

^d The chicks were fed twice when the adults were not observed catching a lemming.

^e The male also caught one Red Phalarope, his total for the day was four lemmings and one phalarope.

One piece of information on the quantity of lemmings fed by a pair of adults to chicks was accidentally obtained in 1956. The female of a pair whose nest was fenced was dead near the nest on 22 July. The male was present, and the two chicks were still alive. There was no food in the nest enclosure. The following morning eight adult lemming carcasses were in the enclosure; that afternoon there were seven lemmings and one Steller's Eider chick (*Polysticta stelleri*). Normally, when one adult catches a lemming both fly to the enclosure and they cooperate in tugging the carcass apart so that both chicks and adults share the prey. In the absence of the female, this male was apparently unable to feed the chicks and the prey simply accumulated in the enclosure. The eight lemmings and one eider chick are a suggestion of the number of prey normally fed to two chicks if we assume that the male had eaten enough for himself. Lemmings in this part of the summer averaged about 50 g (Pitelka, MS). The food brought to the enclosure totaled about 450 g, allowing 50 g for the eider chick, and approximately equals the food consumed by the captive chicks.

The best information on lemming consumption by adult jaegers was obtained by observing breeding pairs for 24-hour periods in 1956 and 1960 (Table 6). The 24-hour watch made on 18-19 June and the two on 7-8 July, were in the incubation period and indicate approximately seven lemmings consumed by a pair of adults. The average weight of 107 lemming specimens from June and early July in 1956 was about 72 g (Pitelka, MS). The weight of seven lemmings eaten by one pair of adult jaegers in 24 hours was then about 500 g, or 250 g each. This seems very reasonable when compared with 200 to 220 g eaten by full sized chicks in captivity.

Two 24-hour watches made when chicks were being fed (23-24 July, and 13-14 August) indicated an average of approximately six lemmings consumed per pair. According to what we know of consumption rates of captive chicks this is much too low. It is possible that the presence of observers inhibited the adults from normal hunting activity or from visiting the chicks. Therefore the food consumption rate of 500 g per day per pair, determined for the first half of the season, was presumed to be constant for the entire season, and was also used as the adult consumption rate for the second half of the season.

The number of lemmings eaten by a successful Pomarine Jaeger family was calculated from these data on food consumption. Two chicks consume the equivalent of 20,000 g of

TABLE 7
SEX RATIO OF LEMMING PELTS FROM POMARINE PELLETS

Date	Males	Females	Per cent males	Per cent females	Totals
<i>1956. chick pellets</i>					
21 July	20	15	57	43	35
25	19	23	45	55	42
29	14	20	41	59	34
14 August	12	20	38	62	32
Total	65	78	46	54	143
<i>adult pellets</i>	104	118	47	53	222
Total	169	196	46	54	365
<i>1960. chick pellets</i>					
12 July	39	34	53	47	73
16	59	48	55	45	107
20	86	60	59	41	146
25	62	49	56	44	111
30	71	64	53	47	135
4 August	58	38	60	40	96
8	15	20	43	57	35
17	12	20	38	62	32
Total	402	333	55	45	735
<i>adult pellets</i>	33	33	50	50	66
Total	435	366	54	46	801

lemmings from hatching to 31 August. Using size class distribution of femurs in pellets as indicating the size classes of lemmings taken in that period (Fig. 3, Table 4), it was calculated that two jaeger chicks would have eaten 339 lemmings in 1956 and 319 in 1960.

The lemming consumption by adult jaegers was calculated for two time intervals. One interval from 25 May to 15 July is the period before the eggs hatch and before the young *Lemmus* of the summer generation emerge from the nest. (For the purpose of this analysis, these two events which were actually separated by a short interval, are assumed to occur simultaneously). The second interval from 16 July through 31 August, is the time from hatching to departure from the breeding grounds.

A consumption rate of seven lemmings per day per pair, derived from the results of these 24-hour watches, was used for the first half of the season, giving a total of approximately 364 lemmings taken. This is the equivalent of 500 g of lemmings per day. At this same rate of consumption for the second half of the season, taking into account the shift of the age structure of the lemming population (Fig. 3), a total of 413 lemmings were eaten in 1956 and 366 in 1960. Thus a pair of adults and two chicks eats approximately 1,050 to 1,100 lemmings in one season.

(3) *Sex ratio of lemmings taken.*—In assessing the impact of a predator on a prey population the sex ratio of the individuals removed is as important as the numbers and age classes.

The sex ratio of all prey pelves in both 1956 and 1960 was almost 1:1 (Table 7). Females predominated slightly in 1956 (54 per cent) and males were 54 per cent in 1960. The initial sex ratio in 1956 in the jaeger chick pellet samples favored males, and there was a continuous decline of the proportion of males through the season. Only in the first sample (21 July) did the percentage of males exceed that of the females. In 1960 the sex ratio in the June sample was 1:1. In July and early August samples it was predominantly male, and only in the 8 and 17 August samples did the percentage of females exceed that of the males. Considering the small size of the samples in 1956 we cannot be certain that the shift in the sex ratio is actually as steady as the data indicate, but a trend to a predominance of female prey is indicated in contrast to the results from 1960.

It is known that male lemmings, like other male microtines, range more widely than the females (Thompson, 1955a) and, hence, are presumably more exposed to predation than females are. This fact has been used to explain the predominance of males usually found in raptor pellets. The sex ratio of lemmings in Snowy Owl pellets from Barrow, for example, was 65 males to 35 females (Thompson, 1955a). The Pomarine Jaegers, however, may be obtaining a more random sample of the prey population than raptorial birds such as the Snowy Owl because they appear to use auditory cues in addition to visual cues to locate prey, because they dig their prey out of the ground, and because of their comparatively small territory.

Early in the season when lemmings are abundant and have little cover, jaegers hunt by flying over the tundra between 15 and 25 feet from the surface; and when a lemming is sighted the jaeger lands and grabs it with its bill. The feet are never used. After the ground thaws and after the shallow lemming burrows are open lemmings are less available, and jaegers obtain them primarily by digging them out of the peat soil with their bills. They appear to use both momentary sighting of a lemming and auditory cues to locate areas in which to dig. Two characteristics of northern Alaska coastal tundra make the second hunting method feasible. The surface layer of soil which thaws in the summer, the active layer, is very shallow. In marsh areas, which are the preferred habitat of *Lemmus*, it may be only six inches deep by late summer. Lemming burrows are therefore usually very shallow, in marsh peat they are typically just below the surface. Secondly, the vegetation is rarely more than five to six inches tall at the end of the growing season, and provides relatively poor cover for lemmings.

One other reason why the Pomarine Jaeger should obtain a more random sample of its prey population than the Snowy Owl and other raptors relates to the relative intensity of territory use. At high densities the Pomarine Jaeger has a relatively small territory, approximately 34 acres on the average, and particularly early in the season, it is confined to that area for all of its food gathering. The jaegers hunting effort for an entire season must be intensive, and its prey should ultimately reflect the actual sex ratio of the prey population.

The Snowy Owl, on the other hand, occupies a much larger area, one square mile or more, and does not have to harvest prey as intensively as the jaeger does. The owl apparently relies on visual cues to locate prey and will in the long run probably take more of those lemmings, the males, which are more active on the surface.

The difference in the sex ratio of the jaeger's total prey between 1956 and 1960 is probably explained by different intensity of predation in the two years, as a result of the difference in the number of lemmings present. In 1960 lemmings were plentiful through the season. With a readily available food supply one would expect the jaegers to take a predominance of the more active lemming sex, the male. In 1956 a shortage of lemmings

developed, and hunting was intensified as indicated by a large amount of time that jaegers spent in hunting activities such as walking and digging. Under this hunting pressure the prey taken should tend to reflect the ratio in the population or perhaps even become selective for females. Increased predation of females under these circumstances should result because in the reproductive period the females have nests of young, either on the surface of the ground or in chambers excavated just beneath the surface. A tendency to defend a nest or to remain with the young should increase the chance that a randomly encountered female would be taken by a jaeger over the chance that a similarly encountered male would be taken.

(4) *Timing of predation.*—The lemming population is free of avian predators for the first one and three-quarter to two and three-quarter years after a decline. Avian predators may breed in low to moderate numbers in the third summer following a decline. Little is known of the least weasel in this period; it is rare and never seen or captured except in peak lemming years. Presumably it is an important factor only in the last year of the cycle.

In a lemming-high summer, jaegers are significant as predators on the lemmings for a little more than three months, from late May until the end of August. Snowy Owls arrive earlier, in late April, and are important predators until the end of August, for four and possibly more months. They have been known to winter in areas of high rodent population and so could have a more prolonged effect than any other avian predator. The Short-eared Owl is sporadic in its occurrence in northern Alaska and has not nested in numbers at Barrow since 1953. The Glaucous Gull occurs in moderate numbers along the north Alaskan coast all summer. In lemming years it is seen taking lemmings during spring melt-off. In that brief period the species probably has a significant effect on the lemming population near the coast. The Parasitic Jaeger is relatively scarce at Barrow and is primarily a bird predator. In 1956, a high lemming year, one pair appeared to feed mostly on fish.

Lemmings are most vulnerable to predation in early spring; they have destroyed their vegetative cover, the only remaining cover, the snow, melts rapidly, and their burrow systems remain frozen or full of water and are unusable. Lemmings are so easily taken in spring that some waste by the predators is evident. Thompson (1955a) found 11 to 12 dead lemmings per acre on several mortality plots in June 1953. More than half of these bore the marks of owls, jaegers or weasels. Though most of the wasted animals are eaten eventually, some are probably lost, thus increasing the total removed by the predators.

A large number of Pomarine Jaegers which eventually depart without breeding add to the impact of predation in early spring. The number of excess birds differs considerably between high years. In 1956 excess birds were estimated to be equal to 25 to 50 per cent of the final breeding population, and in 1960 they were estimated to be less than 25 per cent of the breeding population. In 1952 Pitelka (1955a) estimated that excess birds numbered five times the number of breeding birds.

The impact of a pair of breeding Pomarine Jaegers on the lemming population is constant until the eggs hatch in mid-July. Food consumption then increases as the chicks are fed. Consumption by the chicks, and hence by the entire family, peaks when chicks are in their third week and then declines slightly. Young *Lemmus* emerge from the nest in mid- to late July, adding a large number of small lemmings to the prey population when jaeger chicks are

TABLE 8
 TOTAL PREDATOR IMPACT ON A HIGH LEMMING POPULATION AT BARROW

Predator	Age class	Density (Ind./square mile)	Daily food consumption (g/ind.)	Seasons lemming consumption			Total
				(per ind.)	(per acre)		
					25 May to 15 July	16 July to 31 August	
Pomarine Jaeger	Adult	38	250	338	10	21	31
	Young	38	200	167	—	—	
Snowy Owl ^a	Adult	2	250	350	1.3	1.6	3
	Young	7	150	160	—	—	
Least weasel ^b		64	50	100	5	5	10
Glaucous Gull ^c		20	250	125	0.7	—	1
Waste					4	—	4
Totals					21	28	49

^a Data from Watson, 1958.

^b Data from Thompson, 1955*a*.

^c Estimated.

hatching or partly grown; hence, the number of lemmings consumed increases at a proportionately greater rate than the weight of food consumption would indicate.

Predator impact on a lemming high.—I have used the information on food habits to assess the effect of a high Pomarine Jaeger population on lemming numbers in a year such as 1956 or 1960 at Barrow. I have also tried to define the total predation impact by estimating the effect of the other lemming predators (Table 8). Data for food consumption of the Snowy Owl are from Watson (1958). The density of the least weasel is that given by Thompson (1955*a*) for the 1953 season; it is a conservative estimate. Data on Glaucous Gull density are from my own observations; the food consumption of the gull was estimated on the basis of its weight. The estimate of lemmings wasted was from Thompson (1955*a*) for the 1953 lemming high, allowing for the lower lemming population in 1956 and apparent lack of waste in 1960.

The figures in the three right columns of Table 8 are estimates of predation on a single acre of tundra by each of these predators. The number of lemmings consumed are for two halves of the season, for reasons already discussed, with the season's total in the right column. All predation figures are based on numbers per area without adjustment for unoccupied habitat, and thus are the lowest mean densities for the species involved.

The Pomarine Jaeger takes 31 (63 per cent) of the 50 lemmings removed

TABLE 9
HYPOTHETICAL EFFECTS OF PREDATION ON HIGH LEMMING POPULATIONS OF
DIFFERENT SPRING DENSITIES

Lemming density based on individuals per acre			
Spring density/acre	20-30	30-40	40-50
Number of females	12.5	17.5	22.5
Females lost before breeding	10.5	10.5	10.5
Females left to breed	2	7	12
Average embryos	6 ^a	6	6
Young produced	12	42	72
Total adults remaining	4	14	24
Total mid-summer population	16	56	96
Predation loss after breeding	28	28	28
Excess after predation	-12	28	68

^a Datum from Thompson, 1955a.

per acre by all predators. Its great importance as a lemming predator is thus clearly demonstrated.

I have used three broad estimates of spring lemming numbers per acre: 20-30, 30-40, and 40-50 to assess the effect of predation on the summer lemming population, using the impact of minimum predator density in Table 8. The results (Table 9) are a mean minimum figure for the impact of predation, and suggest that total predator load can depress a spring lemming population of approximately 25 per acre but cannot depress a spring lemming population of 35 per acre or above. The results also indicate the decisive effect that predation in the first half of the summer has on subsequent lemming numbers. Early removal of a relatively few females from the population can mean the difference between a reduction of the lemming population in the summer or not, thus emphasizing the importance of a predator like the Pomarine Jaeger which apparently takes a greater proportion of females than do other avian predators.

These calculations indicate that the predation load on the lemming population is significantly large and can depress lemming populations of some densities, thus confirming the observation that the lemming population was indeed depressed markedly in one high year (1956) and not in another (1960) (Pitelka, MS).

The possible effect of predation by the excess jaegers always associated with breeding populations in spring has not been included in the estimate of total predation load. I have no precise data on their numbers, but their impact can be estimated if we assume there are as many as 25 to 50 per cent of the maxi-

imum breeding population and that they are present in the population for ten days. Under these circumstances they would add 0.5 to 1.0 lemmings per acre to the early season predation impact, and reduce the fall lemming population by two to three lemmings per acre. Assuming they were present as long as 20 days would reduce the fall lemming population by three to six lemmings. These figures do not suggest that this extra spring predation is significant in the total predation load; but it could be pivotal in some years.

Lemming mortality from causes other than predation has been ignored in this discussion. Thus, lemming nestling mortality from action of intraspecific factors, spring flooding, and exposure probably account for some additional mortality; and disease and parasitism while not significant (Krebs, 1964) also remove a few.

This argument has been based on a hypothetical population of jaegers with 100 per cent reproductive success. In fact, success is never that high. Yet, the most decisive part of the season as far as impact on the lemming population is concerned is the first half; and in 1956, a very unsuccessful season for the jaegers, most of the pairs which began to breed were still present in mid-July. The decline of the jaeger population did not take place until the late July when food shortage and consequent chick starvation began to occur. Hence, even in a year when the breeding effort of the predators fails, they may have a critical effect on the prey population by their impact before its summer breeding.

DISCUSSION

The role of predation in the lemming cycle.—Most modern students of the lemming cycle reject the idea that the cycle is caused by predators (Krebs, 1964). Predators do kill a large number of lemmings, and Pitelka, Tomich, and Treichel (1955a) suggested that under some circumstances predators could affect the periodicity of the cycle by postponing a population peak from one season to the next. They suggested that in a summer of moderate lemming numbers, in 1952 at Barrow, the predators prevented the lemmings from increasing and postponed the lemming population peak to the summer of 1953.

Current hypotheses are concerned with causative factors intrinsic to the lemming population (Christian, 1950; Chitty, 1952) or are concerned with interaction of the lemming population with its food supply (Lack, 1954; Pitelka, 1957). However, Pearson (1966) studied the effectiveness of mammalian predators on a complete cycle of abundance of *Microtus californicus* and concluded that carnivore predation was "an essential part of the regular cycles of abundance of lemmings, *Microtus*, and other microtines."

According to Pearson mammalian predators are not necessarily important in starting the decline from the population peak, but are important in reducing

the population to the lowest part of the cycle and in maintaining the low population until they themselves starve. Their action accounts for one of the most inexplicable aspects of the lemming cycle; the long delay in recovery from the population low.

Since avian predators are not present in significant numbers during the lemming population build up, their role in the cycle in northern Alaska is practically restricted to their action on the lemming peaks. The evidence presented here shows that avian predators do take a large number of lemmings and that at some lemming densities they can markedly depress the lemming population, while in others they cannot. There is also observational evidence that lemmings may be reduced in numbers by avian predators (1956), or they may increase despite the action of avian predators as in 1960. The events of 1956 demonstrated dramatically that the avian predators cannot be responsible for a complete lemming decline as in that year most of the jaeger chicks starved when it was still possible to snap trap some lemmings. The role of the avian predators in the lemming population cycle in northern Alaska then seems to be the exploitation of the peak population and to truncate the top of the peak by their action.

The role of mammalian predators in the lemming cycle in northern Alaska has not been studied; but the large population of least weasels which occur in the peak summer must persist into winter, and since there is no alternative prey, they must continue to prey on the lemmings remaining after the avian predators depart. Arctic foxes are also usually abundant at the end of lemming-peak summers. They are not usually seen near Barrow in the summer, but in autumn numbers of young of the year are seen apparently foraging for lemmings. Thompson (1955*b*) interpreted the results of his study of the lemming population from 1950 to 1954 at Barrow as being best explained by Lacks' (1954) food hypothesis. Yet he also says (Thompson, 1955*b*, p. 173) that "our field evidence strongly suggests that it is the continued pressure by weasels through the winter which eventually reduced the lemmings to the extremely low numbers of 1950 to 1954. As lemmings declined in abundance, the owls, jaegers, and foxes emigrated and shifted to other food, but the weasels' only alternative was to extend their efforts in pursuing the remaining lemmings." Maher (1967) presented evidence that a low to moderate winter population of lemmings was almost destroyed by predation by ermine on Banks Island, N.W.T. These observations strongly suggest that predation, particularly by weasels, may in fact be responsible for the great decline of lemmings in the winter after a peak summer in northern Alaska, and thus may be causing the population cycle.

Evidence from the eastern North American arctic is not as suggestive, but

both Krebs (1964) and MacPherson (1966) working in areas where the two lemming species (*Lemmus* and *Dicrostonyx*) occur together in a mosaic of habitats which bring them in close proximity found that their populations cycled synchronously. Synchrony of the two species suggests some external action tending to keep them in phase, and predation by mammalian predators is a very possible responsible factor, although Krebs (1964) rejected this possibility.

The possibility that the action of mammalian predators in reducing the population and prolonging the low is responsible for the cycling of the lemming population now seems tenable and should be studied further.

SUMMARY

Food habits, breeding density, and breeding success of Pomarine Jaeger populations nesting in response to different spring densities of the brown lemming population were studied at Barrow, Wainwright, Pitt Point, and Cape Sabine, northern Alaska. Food habits of nonbreeding populations were studied for comparison with breeding populations.

When Pomarine Jaegers breed, their food supply is at least 80 per cent lemmings with birds the next most important food category. Lemmings occurred in less than half of the stomachs of nonbreeding populations, suggesting that the jaeger cannot obtain enough food to support breeding unless there are enough lemmings to provide most of its food.

Jaeger breeding density correlated with spring density of the brown lemming up to a maximum density of approximately 19 pairs per mile. Three lemming highs (1953, 1956, and 1960) supported virtually identical mean Pomarine Jaeger densities although lemming density differed between peak years.

Breeding success was low at low breeding densities and low to moderate at intermediate densities. At maximum density, breeding success ranged from almost complete failure (1956) to high success (1960).

The size classes of lemmings in the jaegers' diet was determined from the length of femurs in regurgitated food pellets of adults and chicks. The number of prey taken was determined by the amount of food eaten by chicks raised in the laboratory, and by several 24-hour watches of jaeger pairs. The sex ratio of lemming prey was determined from the pelvis in jaeger pellets.

Calculations from these data indicate that a pair of jaegers raising two chicks in a year of maximum jaeger density remove an average of 31 lemmings per acre from their territory in the season. Other predators remove an additional 18 for a total of 49 lemmings removed per acre by the action of all predators. This is sufficient to depress a lemming population of approximately 25 per acre in the spring but not a population of 35 per acre or above.

The role of the avian predators in the lemming cycle is to truncate the peak populations, but they are unable to reduce the lemming population to the low point of the cycle. It is suggested that mammalian predators, especially *Mustella rixosa*, are responsible for reducing the population completely and delaying recovery of the lemming population until they themselves decline in numbers.

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A POPULATION ESTIMATE OF THE DUSKY SEASIDE SPARROW

BRIAN SHARP

DURING the spring of 1968 I attempted to determine the absolute numbers and distribution of the Dusky Seaside Sparrow (*Ammospiza nigrescens*), which has been regarded as threatened with extinction (Bureau of Sport Fisheries and Wildlife, 1966). Most of the few completed world population censuses of birds fall into four general types: those concerning (1) large and conspicuous species, often water birds, and often lending themselves to aerial census and photographic techniques, such as the North Pacific albatrosses (Rice and Kenyon, 1962); (2) populations that gather into few traditional breeding or wintering concentrations, such as the Gannet (Fisher and Vevers, 1944); (3) conspicuous endangered species, of at least seasonally restricted distribution, such as the California Condor (Miller, McMillan and McMillan, 1965); and (4) less conspicuous species of a very restricted distribution, often on islands, like the Takahe (Williams, 1952). The Dusky Seaside Sparrow, confined to the salt marshes of Brevard County, Florida, falls into this last category. For a review of the early literature on total-bird-population censuses, see Fisher (1954).

HISTORY

Ammospiza nigrescens was discovered in 1872 around Salt Lake on the Florida mainland (Fig. 1) (Maynard, 1875), where it was presumably always rare (Chapman, 1899). Certainly it has not been seen there since (Baynard, 1914; Charles H. Trost, in litt.). Maynard found the species abundant on the salt marshes of the northern half of Merritt Island, and Chapman (1899, 1912) reported it there from Banana Creek to the mouth of Dummitt Creek (see also Baynard, 1914; Vars, 1926). Charles E. Carter, a friend of the late D. J. Nicholson, told me that it was not uncommon for the latter to find 30 Dusky nests in a day's egg-collecting in just that part of the salt marsh across the bridge from Titusville. In addition, Nicholson (1929) reported a colony of 20 pairs on the mainland, 1½ miles east of the St. John's River, due west of Indian River City. Since 1957, the Merritt Island salt marsh has been impounded for mosquito control (for vegetation changes, see Provost, 1959; Trost, 1968) with the result that by 1961-63 the Dusky Seaside Sparrow population had been reduced to (a minimum of) four aggregations totaling approximately 70 pairs (Trost, in litt.). Trost also found that the colony on the mainland had dwindled by 1962 to about five pairs, and subsequently these birds disappeared entirely (Bureau of Sport Fisheries and Wildlife, 1966:B-49). *A. nigrescens* is



FIG. 1. Present and former distribution of the Dusky Seaside Sparrow, Brevard County, Florida.

at the moment on the rare and endangered species list of the U. S. Fish and Wildlife Service (ibid.). It was because of this critical situation that the present study was undertaken.

METHOD

The census method was the singing-male count, which is most efficient for inconspicuous small birds in dense cover, where flushing distances are short and the habitat extensive. However, the method has two major disadvantages: it is less than 100 per cent efficient, and variably so. When one visits a given nesting area, only a certain proportion of the total males present will be singing, depending upon the stage of the breeding eyele, time of day, climate, and weather. This proportion, designated *effectivity* by European ornithologists (Enemar, 1959; Williamson, 1964) is a refinement of Colquhoun's (1940) "coefficient of conspicuousness" (see also Palmgren, 1930; Hickey, 1943:83; Nee, 1943:122-

4). Effectivity is determined by repeatedly visiting, at different times of the day, a number of colonies (whose total male population becomes known in the process) and by mapping the males recorded. The percentage of males recorded singing on any one visit is the effectivity, or efficiency of the census (hereafter designated "Ef"). To increase sample size Ef data were on a few occasions gathered from study areas censused only twice, and the population was taken to be the number seen on the highest count, the lower count being compared to this for the purpose of effectivity. If the summation method of Palmgren (1930:93) is used in conjunction with the mapping method, the higher of the census figures can also be used for Ef, this being compared to the non-overlapping composite of the two or more counts. Ef tends to be overestimated if the area has not been censused at least three or four times and the locations of singing males mapped.

Most of the area was covered on foot, part on horseback, and part by bicycle. A helicopter was used to determine the simple presence or absence of the Dusky Seaside Sparrow in some of those areas not covered from the ground due to lack of time. If one flies at 100 ft at 30 mph over the marshes, all species of birds flushed, including passerines, can be identified from prior field experience on the ground. The Dusky Seaside Sparrow is distinctive, especially in flight, and could be carelessly confused only with the female Red-winged Blackbird (*Agelaius phoeniceus*).

THE AREA

For a description of typical salt marsh habitat on Merritt Island, see Nicholson (1928:229) and Trost (1968:851). The Dusky Seaside Sparrow uses the restricted zone where the short grass *Distichlis spicata* and the tall *Spartina bakeri* interdigitate, producing a heterogeneous pattern. For a botanical treatment of the St. John's marshes, including a point-quadrat analysis, see Sincock (1958). The marshes on the mainland between Routes 520 and 46 are dominated by salt-marsh plants, primarily *Spartina bakeri*, and dotted with palm trees (*Sabal palmetto*) and hammocks, so that the total aspect is savannah-like. Water levels and salinities vary considerably with the precipitation pattern, with a corresponding variability in the height and density of the *Spartina*, thus providing diversity of bird niches within the same tall-grass life form. Because salinities are low at times of high water, a number of freshwater marsh plants add variety to the vegetation but are never dominant. The mainland salt marsh owes its existence to Pleistocene interglacial invasion by marine waters below the 20-ft contour line, when salt was deposited in the sediments (Odum, 1953). Usually much of the St. John's is inaccessible, but 1968, the second year of a general Florida drought, was opportune for the purposes of census.

RESULTS AND DISCUSSION

Figure 2 shows the bimodal effectivity curve as a function of the time of day, the peaks occurring in the early morning and evening. The discrepant Ef (86 per cent) for the hour of 12:00–12:59, based on one observation period during and after a light rain, was due to the vigorous resumption of singing characteristic of the species under such conditions (Trost, 1968:852). The maximum average Ef figure of 73 per cent for the early morning agrees surprisingly well with Enemar's effectivities for the Willow Warbler (*Phylloscopus trochilus*) (73 per cent), Garden Warbler (*Sylvia borin*) (73 per cent), Ortolan Bunting (*Emberiza hortulana*) (65 per cent), etc. (Enemar, 1959:32).

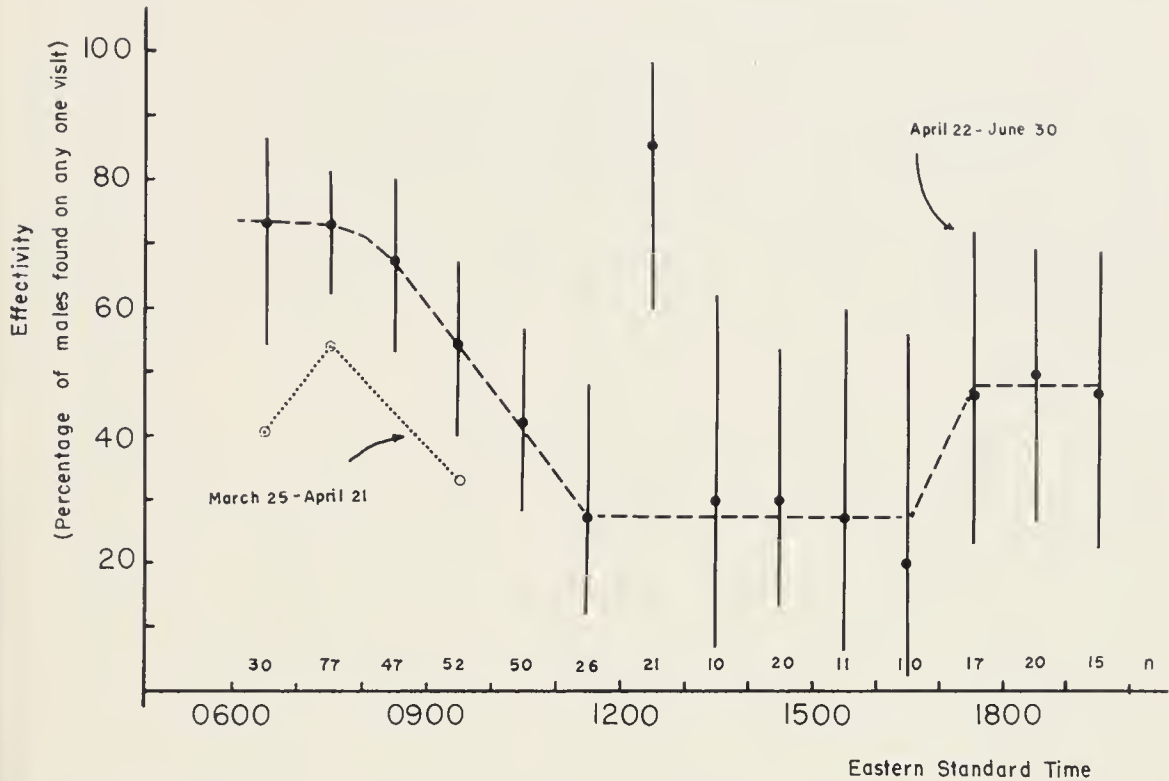


FIG. 2. Efficiency of the census (effectivity) expressed as a function of the time of day. Vertical lines through the means are confidence limits (95 per cent), n is sample size for the line of 22 April-30 June. Curve is drawn in visually.

but is less than the 88 per cent for the American Woodcock (*Philohela minor*) (Duke, 1966; Sharp, unpubl.), whose activities are concentrated into a short crepuscular period. In contrast to the present study, Enemar (1959:27) found that effectivities were almost constant throughout the day, this perhaps being a reflection of the more uniform Swedish woodland climate. This and the fact that a shower can stimulate singing in the middle of the day imply that the pattern of singing activity is not part of a circadian rhythm, but is a function of microclimatic conditions, specifically, in an exposed salt marsh, either of the oppressiveness of the heat or of light intensity. Ricklefs and Hainsworth (1968) report on the temperature-dependent behavior of the Cactus Wren (*Campylorhynchus brunneicapillus*), which selects cooler microhabitats increasingly toward early afternoon, unless cloud cover allows the birds to frequent more exposed areas. One of the reasons that the effectivities for *nigrescens* are as high as they are in the middle of the day (27 per cent) is the effect of either the bird detecting the observer or being flushed by the observer walking through the grass, after which males had a tendency to sing briefly, stimulating their neighbors to do the same. Spontaneous sporadic outbursts of territorial behavior also occur (Nicholson, 1928:228), interrupting the general midday silence and raising the average Ef.

Due to an atypical coolness of the spring, effectivities were lower, although not significantly so, during the first four weeks of the singing period than during the second and third four-week periods, between which there was no difference. By summer, singing intensity is reported to diminish markedly (cf. Davis, 1965). There was no difference between the effectivities of the Merritt Island and the St. John's birds, even though densities were significantly different (6.7 ± 0.6 and, in the best areas, 3.0 ± 0.3 acres/bird, respectively, $P = 0.05$).

THE CENSUS

Merritt Island National Wildlife Refuge.—On Merritt Island, traditional haunt of *nigrescens* and mecca for birdfinders (Pettingill, 1951:85), six weeks of repeated searching and territorial mapping revealed a remnant population of 33–34 males, all but 4 or 5 of which were located in breeding aggregations of 7, 8, and 14 birds. This represents a decrease of at least 50 per cent over the past 5 years. In 1968 these 29 males occupied 200 acres of remaining suitable salt-marsh vegetation at the above-mentioned comparatively low density. Another two males, apparently unmated, were attempting to subsist on small territories of 1.1 and 0.8 acres, and at least two wandering males did not have permanent territories at all. Of 7,565 acres of impounded salt marsh only about 6,000 were originally suitable habitat for the Dusky Seaside Sparrow if one assumes that the birds had to be within a certain distance (2,300 ft) of the tidal zone either for feeding (Tomkins, 1941; Trost, 1968:852) or for reasons of habitat selection (the grass *Distichlis* occupies a lower place in the salt-marsh plant zonation: Chapman, 1960:256–9). If one assumes also that their former density was similar to that now found on the St. John's River (perhaps an underestimate, cf. Trost, 1968:852) and that all suitable habitat was filled, an estimate of the former population on Merritt Island is of the order of 2,000 pairs. This seems not unreasonable in view of the above testimony to the former abundance of the bird.

St. John's River.—In May and June, 372 singing males, many of which were paired, were found on the St. John's River marshes in breeding aggregations of various sizes, 95 in the largest. In Table 1 the number of birds found at any particular time of day is divided by the corresponding known Ef figure to arrive at a more realistic population estimate. For convenience, some of the not significantly differing Ef values of Figure 1 have been lumped, and 14 birds found by revisiting colonies were excluded as these were accounted for by means of Ef. Thus 358 males found actually represent about 641 males in the area searched. Of these 358, all but 33 were found between the 10- and 15-ft contour lines of the USGS quadrangles, and none above 17–18 ft. Above this elevation the marsh is often dry enough for invasion by *Sabal palmetto*

TABLE 1
THE NUMBER OF MALES FOUND IN THE ST. JOHN'S RIVER MARSHES AT VARIOUS HOURS
OF THE DAY CORRECTED FOR EFFECTIVITY

Eastern Standard Time	No. of males found	Effectivity		Corrected no. of males		
		Mean	95 per cent limits	Mean	95 per cent	
					Lower	Upper
06:00-08:59	217	0.71	0.63-0.78	305.6	278.2	344.4
09:00-09:59	40	0.54	0.40-0.68	74.1	58.8	100.0
10:00-10:59	29	0.42	0.28-0.57	69.0	50.9	103.5
11:00-16:59	31	0.27	0.18-0.38	114.8	81.6	172.2
	9	0.86	0.60-0.98	10.5	9.2	15.0
17:00-19:59	32	0.48	0.34-0.62	66.7	51.6	94.1
	358			640.7	530.3	829.2

and is susceptible to burning, while below 10 ft the flooding of the river probably sets a lower limit to colonization. Ninety-five per cent of the Dusky Seaside Sparrow nests ($n = 39$) are located between 10 and 13 inches above the ground, but two weeks after the near hurricane of 3-5 June which deposited 14 inches of water, there were still 2 ft of water below the 10-ft contour, whereas a number of other revisited colonies were for the most part on dry ground. The day after the hurricane, water depth in one colony was 5-7 inches. On Merritt Island, where the effect of the tides (except wind tides) is negligible, the seaside sparrow has evidently lost the habit of nesting higher. In comparison, the New Smyrna Seaside Sparrow (*A. maritima pelonota*), with a former colony located at the mouth of a tidal inlet, builds a nest whose average height above the ground was 19-26 inches (95 per cent limits, $n = 24$). (These and the above nest data were taken from the slips for the egg collections of the late Charles E. Carter, Orlando, and Clemson University, Clemson, South Carolina.) The river is used by cattle for drinking water in the dry season; consequently, areas below 10 ft tend to be heavily grazed.

Using a planimeter, large-scale (1 in. = 400 ft.) aerial photographs (flown 1967), and USGS quadrangles for reference to contour lines, I measured the areas searched, left unsearched, less than 10 ft, 10-15 ft, and above 15 ft (Table 2). The 641 males occupied an area of 2,980 acres, with an overall density of 4.65 acres/male. Of the unsearched habitat which appeared suitable from the aerial photographs, most of which lay between 10 and 15 ft, and in one area of which a Dusky Seaside Sparrow was flushed by the helicopter, there are possibly another 629 males. This, however, represents a maximum number because field investigation will prove some of this area unsuitable. Much

TABLE 2
ESTIMATE OF THE DUSKY SEASIDE SPARROW POPULATION IN THE ST. JOHN'S MARSHES,
SPRING, 1968

Habitat	Acres	Corrected no. of males		No. of acres per male	
		Mean	95 per cent limits	Mean	95 per cent limits
Searched					
No. present	2983 ¹	641	530-829	4.65	3.60-5.63
No. absent	5941 ²				
Unsearched					
Good: 10-15 ft, ungrazed, unburned	976 ³	210	173-271	4.65	3.60-5.63 ⁴
Poor: 10-15 ft, grazed or burned	287 ³	43	39-47	6.7	6.1-7.3 ⁵
Unlikely: <10 ft, or >15 ft	843	—	—	—	—
Total		894	742-1147		

¹ Almost all 10-15 ft above sea level.

² 513 acres <10 ft, 4433 acres 10-15 ft, and 995 acres >15 ft.

³ 40.2 per cent of the actual acreage, based on the fact that 59.8 per cent of searched habitat between 10 and 15 ft was either unsuitable or unfilled.

⁴ Assumed to be the same as the density in searched habitat.

⁵ The density of the Merritt Island population.

of the St. John's is grazed by Brahma cattle and burned by ranchers to provide higher-quality forage. By the second or third year after burning, the grass is high enough again to be utilized by the Dusky Seaside Sparrow, but it is impossible to say with certainty from aerial photographs alone what conditions will be actually encountered. A second reason for habitat proving unsuitable is the fact that the Dusky occupies a middle position along a moisture gradient where the density of the *Spartina* is 1741 ± 24 stems/m² and the height 3.05 ± 1.29 ft ($P = 0.05$). Numerous references in the literature testify that the habitat of the Dusky Seaside Sparrow is somewhat drier than most salt marshes, and on the St. John's this preference is evident from the bird's distribution. The bird is usually absent from wetter low places where the *Spartina* is more dense; and in the driest areas where the *Spartina* is shorter and thinner, *nigrescens* is replaced by the Eastern Meadowlark (*Sturnella magna*). Further, the breeding distribution of *nigrescens* tends to be aggregated due to social tendency (cf. Tomkins, 1941 for *A. m. macgillivraii*). For these reasons, I found that about 60 per cent (4,434 acres) of the *Spartina* marsh was either unsuitable or unfilled, which proportion probably applies to unsearched habitat. Therefore, the possible 629 additional males should be reduced to a probable 253 (95 per cent limits 213-318). The total number of male *nigrescens*

on the St. John's, actual and probable, is about 894 (95 per cent limits 742-1147).

SUMMARY

A singing-male census of the endangered Dusky Seaside Sparrow, conducted in the spring of 1968, revealed a remnant population of 33-34 males on Merritt Island and a heretofore unknown population of 372 males in the St. John's River marshes between Routes 520 and 46 on the east side of the river. Efficiency of the census varied from 73 per cent (95 per cent confidence limits 63-82 per cent) from 06:00-08:00, dropping gradually throughout the morning to a low of 27 per cent (18-38 per cent) from 11:00 to 17:00, and rising again in the evening to 48 per cent (34-62 per cent). Therefore, the St. John's figure of 372 actually represents about 641 males (95 per cent limits 530-829). An additional 253 males probably exist in unsearched habitat.

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AN INVESTIGATION OF TERRITORIAL BEHAVIOR IN THE AMERICAN REDSTART UTILIZING RECORDED SONGS

ROY A. ICKES AND MILLICENT S. FICKEN

THE territorial behavior of the American Redstart (*Setophaga ruticilla*) has been studied by Hickey (1940), and in greater detail by Ficken (1962). Hickey has described this species as being "highly territorial," defending an area by song and formalized displays. Ficken has described the territory as being maintained during the breeding season with both sexes usually remaining completely within it; the male defends the area against other male redstarts. The objective of this investigation was to examine experimentally territorial aggression in male American Redstarts in relation to their breeding condition, the size of their territory, and the location of an encounter within their territory. The area and changes in size of redstart territories were also studied.

These factors and their effect on territorial behavior in other birds have been examined in a number of studies. The nature of encounters in territorial male Ovenbirds (*Seiurus aurocapillus*) varied as the breeding cycle of the birds progressed (Weeden and Falls, 1959). The fact that a territory is defended with increased vigor the smaller its size and the nearer the intruders approach its center has been recorded (e.g., Bremond, 1963; Armstrong, 1965). Evidence that territories are compressible but that a minimum size appears to exist has been presented by Huxley (1934) and more recent investigators have elaborated on his ideas (Tinbergen, 1957). Observations of the effect of these factors on the response of a territorial male redstart have been referred to in several studies (Ficken, 1962; Ficken and Ficken, 1965), but this particular aspect of redstart behavior has not previously been studied experimentally.

Several field studies have shown that tape-recorded songs and calls are stimuli sufficient to evoke behavior which normally occurs in response to the singing of another bird (e.g., Weeden and Falls, 1959; Stein, 1963). Bremond (1963) has stated that the reaction of a territory owner to a previously recorded song was immediate and definite; the bird would approach and sing near the loudspeaker.

MATERIALS AND METHODS

This study was conducted at the Patuxent Research Refuge, Anne Arundel and Prince Georges Counties, Maryland. The habitat consisted of areas with an understory of bushes and young trees 5-20 feet high with much herbaceous undergrowth. Such habitat has been considered typical for this species (Griscom and Sprunt, 1957; Ficken, 1962). Male redstarts on adjacent territories were recognizable as individuals by differences in color pattern, eliminating the need for color banding.

In the spring of 1967 two phases in the breeding cycle of the redstart were studied. One series of experiments was conducted from 24 April to 4 May before the males had acquired a mate (pre-mating); the second series, 10 May to 21 May, was run between the time a mate was acquired and the end of nest building (post-mating). In a study of courtship in the redstart, Ficken (1963) observed that "A female never left a male after she once remained for as long as an hour." Therefore, we considered a bird mated if a female was present in the territory of a male during the major portion of an observation period (i.e., one hour). In all cases this criterion proved to be a valid indication of subsequent and continued matedness of the male.

The redstart possesses two song types: an Accented Ending Song (A) and an Unaccented Ending Song (U) which apparently differ in motivation and function (Ficken and Ficken, 1965). Since an analysis of these song types by Ficken and Ficken (MS) showed that playback of the A-type song usually induced significantly closer approaches to the speaker than playback of the U-type song, an Accented Ending Song obtained from the Federation of Ontario Naturalists Warbler Record was used in all the experiments. The playback tape consisted of a six-minute sequence of six repeats of the song per minute. An Uher 4000 S portable tape recorder and a Nagra DH amplifier-speaker were used. The volume of the speaker was maintained at maximum level and could be heard 200 feet away by the observers; during all playbacks the redstarts were within 100 feet of the speaker.

Several days before the redstarts were expected to arrive at the Refuge, a pre-determined study area of approximately 20 acres was staked out. When a male redstart was first seen in the study area during phase I (pre-mating), it was observed for at least one hour and each tree that it flew into was marked. (Each bird sang from most of the trees it visited.) The marked trees were plotted on a sketch map of the area and the locations of encounters with other male redstarts were recorded. Each of the plotted points on the sketch map of the bird's activities was connected to all the other plotted points by a straight line. The area of the polygon thus formed was calculated with a compensating polar planimeter and will be referred to as the bird's maximum utilized territory. A redstart's activities appeared to be restricted to this specific area and it advertised its presence within it by singing. Although not enough territorial disputes were observed to state clearly that this entire area was defended in the strictest sense, all observed intrusions by other male redstarts were repulsed by the owner of the utilized territory.

In both the pre-mating and post-mating phases, the redstarts were observed during the playing of the stimulus tape in the center of each bird's maximum territory, and somewhere on the periphery of the territory. Approximately 24 hours separated the peripheral and center playback experiments for each bird. All the experiments were conducted between 07:00 and 11:00 EDT, and the time for each series of playbacks for a given bird was kept as constant as possible (i.e., within a range of two hours).

When a bird had moved into a desired location for a playback, the speaker was placed on the ground about 50-100 feet away from the bird. After the equipment was set up the bird was watched for six minutes, during which its vocalizations and distance from the speaker were noted. If the bird remained within 50-100 feet of the speaker during this period, the six-minute stimulus tape was played. After each stimulus song the location of the bird in relation to the speaker was noted as were his vocalizations. The next day before an experiment was initiated, the bird was observed for 30 minutes to be sure no changes in territory size had occurred and that the bird had not acquired a mate.

During phase II (post-mating), the movements of the male redstarts were observed for approximately an hour before the first playback was conducted and shifts in the shape

TABLE 1
APPROACH LATENCY

Bird	Pre-mating		Post-mating	
	Periphery	Center	Periphery	Center
A	(>36)*	(>36)*	24	16
B	6	13	23	29
C	33	11	19	4
D	10	5	(NE)**	(NE)**
E	13	4	8	6
F	9	12	17	12
G	31	4	16	15
H	(>36)*	(>36)*	(>36)*	(>36)*
I	6	9	3	10
J	1	2	2	8
K	(NE)**	(NE)**	4	3
Median	11.5	10	16.5	11
60 percentile	6-33	4-13	4-23	6-16

* No approach within 30 feet during 36-song playback experiment.

** No experiment performed.

No significant differences between paired comparisons.

and maximum size of the territory were noted. The peripheral and center playback procedure in this set of experiments was the same as that used during phase I (pre-mating).

During the course of the six-minute playback, a reactive redstart would fly toward the speaker usually giving some type of vocalization. The bird would approach the speaker in an ambivalent manner, moving closer and then farther away, occasionally flying over it. The exact nature of the response was variable: some birds would approach the speaker almost immediately, others would not; some would sing each time the stimulus song occurred, while others were considerably less vocal. Therefore, three criteria of responsiveness were used: the number of songs played back before the bird approached within 30 feet of the speaker (approach latency), the number of songs played back during which the bird was within 30 feet of the speaker (approach duration), and the number of times a bird flew over the speaker divided by the number of songs played back during which the bird was within 30 feet of the speaker (flights over speaker). The criteria, flights over the speaker was handled this way in order to maintain the independence of the three criteria. In other playback studies, variants of these criteria have been utilized (c.g., Weeden and Falls, 1959).

With the use of the Wilcoxon matched-pairs signed-ranks test, a comparison was made between the birds' responses to peripheral playbacks and their responses to center playbacks. The data obtained during pre-mating and post-mating were treated separately and a comparison of peripheral versus center responses was carried out for each criterion.

RESULTS

Measures of responsiveness.—The data for the redstarts' responses are shown in Tables 1-3. Eleven birds were tested: nine birds were tested during pre-mating and post-mating; one was tested only during pre-mating (it

TABLE 2
APPROACH DURATION

Bird	Pre-mating **		Post-mating	
	Periphery	Center	Periphery	Center
A	0	0	7	10
B	16	24	9	8
C	4	6	4	29
D	20	27	(NE)*	(NE)*
E	4	6	29	6
F	4	16	3	8
G	6	21	13	22
H	0	0	0	0
I	12	6	20	12
J	12	24	35	27
K	(NE)*	(NE)*	33	34
Median	5	11	11	11
60 percentile	3-12	6-24	4-29	8-27

* No experiment performed.

** $0.05 > p > 0.02$ (Other paired comparison not significant.)TABLE 3
FLIGHTS OVER SPEAKER

Bird	Pre-mating **		Post-mating	
	Periphery	Center	Periphery	Center
A	0	0	0.14	0.20
B	0.06	0.08	0.22	0.25
C	0.25	0.33	0.25	0.14
D	0.20	0.56	(NE)*	(NE)*
E	0.25	0.17	0.17	0.17
F	0.50	0.63	0.33	0.38
G	0.17	0.33	0.15	0.09
H	0	0	0	0
I	0.17	0.50	0.10	0.08
J	0.67	0.79	0.34	0.30
K	(NE)*	(NE)*	0.12	0.24
Median	0.185	0.33	0.16	0.185
60 percentile	0.06-0.25	0.08-0.56	0.12-0.25	0.09-0.25

* No experiment performed.

** $0.05 > p > 0.02$ (Other paired comparison not significant.)

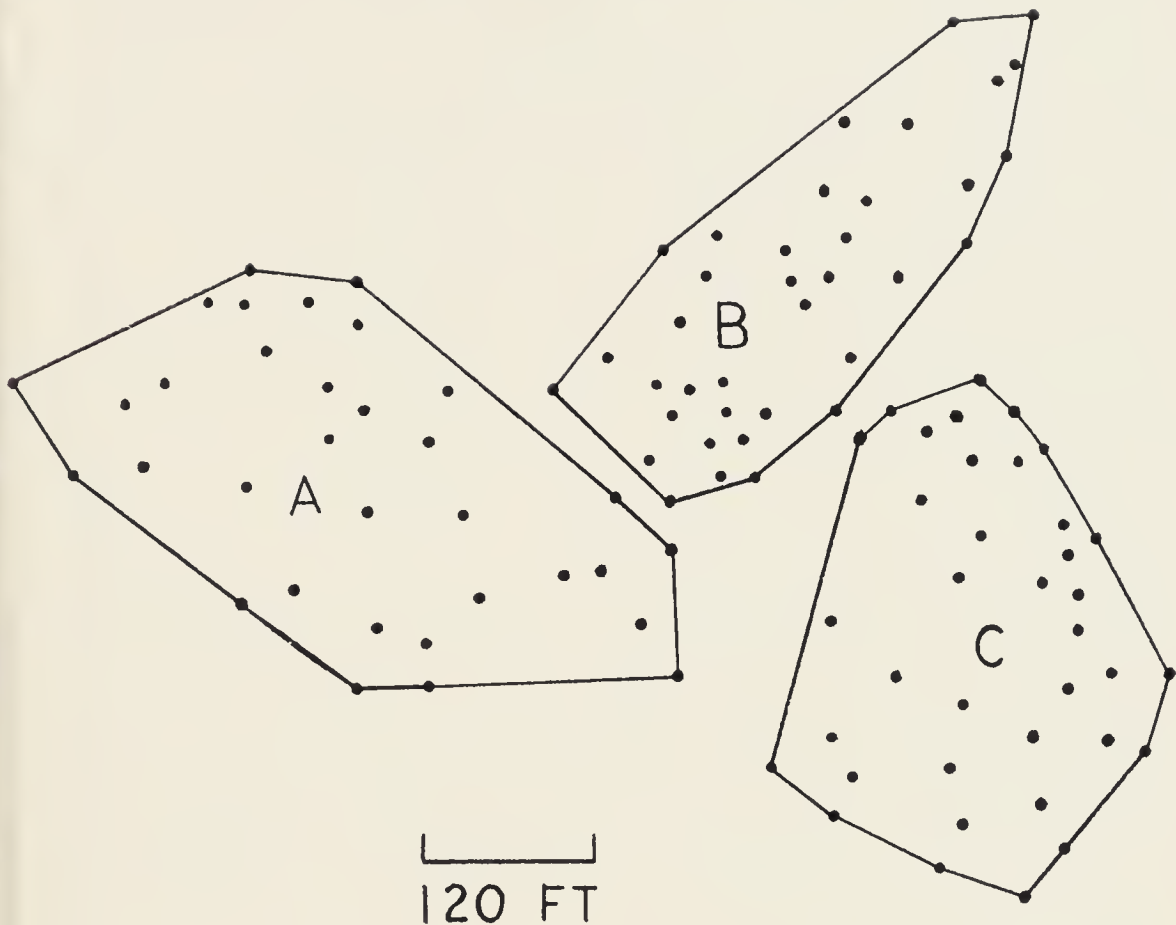


FIG. 1. Sketch map depicting maximum territories of unmated birds (pre-mating). The letters denote the birds identified in Tables 1-4. The black dots represent the trees a redstart visited during the one-hour observation period.

abandoned its territory and another bird was substituted and tested only during post-mating).

The data for approach latency (Table 1), showed no significant difference between the responses to peripheral and center playbacks either during pre-mating or post-mating. During pre-mating there was a significant difference in approach duration ($0.05 > p > 0.02$) between the birds' responses to peripheral and center playbacks. They remained within 30 feet of the speaker for a longer period of time during the playbacks in the center of their territories. Similar results were obtained for the flights over the speaker criterion (Table 3). During pre-mating there were slightly but significantly more ($0.05 > p > 0.02$) flights over per unit time in response to center playbacks compared to peripheral playbacks. During post-mating there was no significant difference between the responses to peripheral and center playbacks either in approach duration or in the number of flights over per unit time.

Maximum territory size and shape.—Figures 1-2 are examples of the

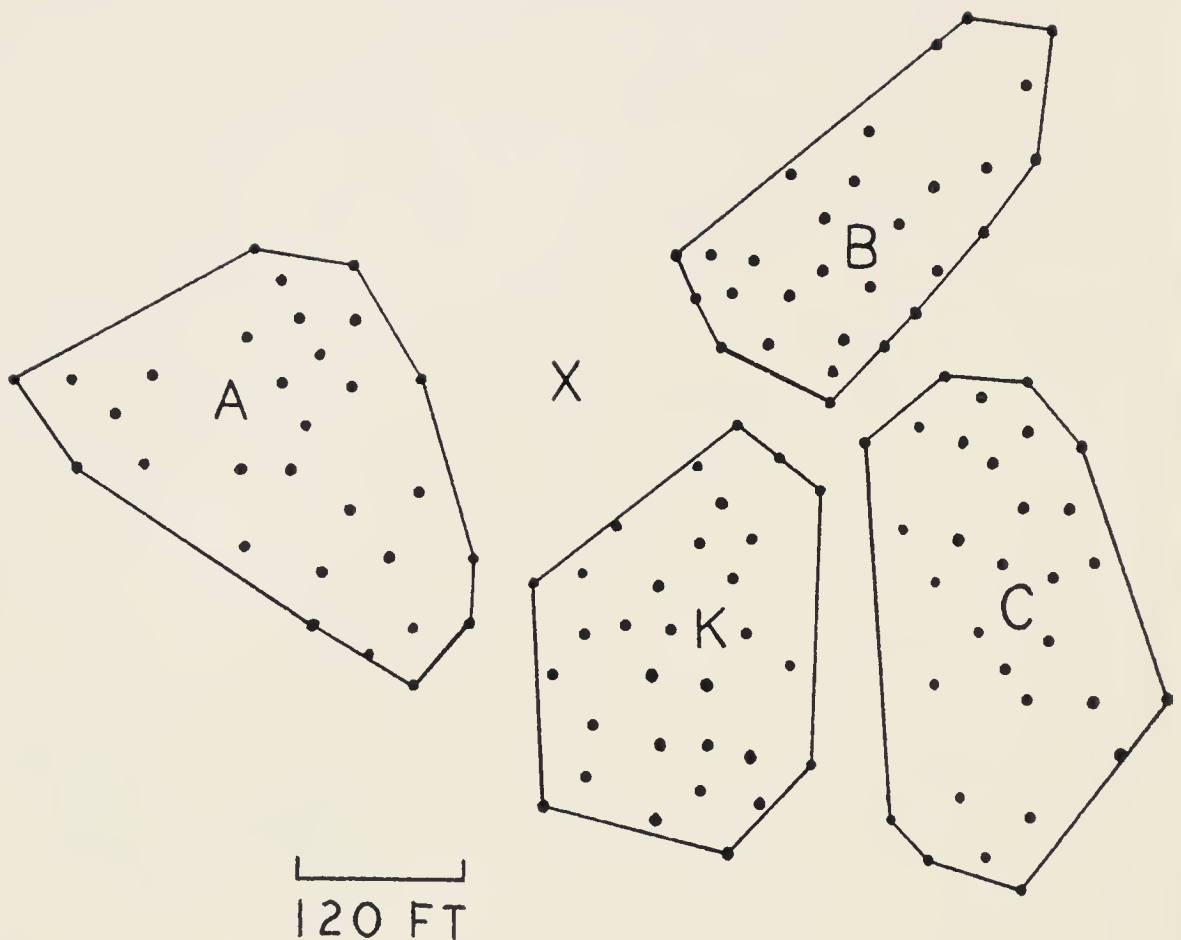


FIG. 2. Sketch map depicting maximum territories of mated birds (post-mating). The letters denote the birds identified in Tables 1-4. The black dots represent the trees a redstart visited during the one-hour observation period. The X indicates the approximate area occupied by a very late arriving bird not considered in this study.

sketch maps which show the territories the male redstarts held, and the territory size of each bird before and after mating is given in Table 4. The mean size before mating was 1.49 acres, and after mating was 1.13 acres. For six birds the territory size before mating was larger than after mating, the size of one bird's territory increased after mating, and in two birds there was no observed shift in territory size. The mean amount of shift in territory size for these nine birds was -0.32 acres.

DISCUSSION

Before a redstart acquired a mate, there was a significant difference between the defense of a territory's periphery and its center in two of the approach measures of responsiveness. The approach responses of the male in the center of his territory were more aggressive than those in the periphery (i.e., he remained near the speaker longer and flew over it more often per unit time in the center). However, between the time of pair formation and

TABLE 4
TERRITORY SIZES

Bird	Size before mating acres	Size after mating acres	Amount of shift in size acres
A	1.24	0.84	-0.40
B	1.57	1.29	-0.28
C	1.97	1.32	-0.65
D	1.77	*	—
E	2.01	1.41	-0.60
F	2.26	1.45	-0.81
G	1.17	0.92	-0.25
H	0.66	0.77	+0.11
I	1.00	1.00	0
J	1.24	1.24	0
K	*	1.09	—
Mean	1.49	1.13	-0.32

* No observations.

the end of nest building (post-mating), the redstart defended the periphery and the center of its territory about equally. Table 2 suggests that post-mating responsiveness is more like the intense pre-mating responsiveness at the center than the less intense reactions at the periphery.

The fact that a bird will defend its territory with increased vigor the nearer an intruder approaches its center has been noted on a number of occasions (e.g., Lorenz, 1938; Bremond, 1963), and this might be the type of reaction observed in this study. However, this does not explain why the redstarts were more aggressive in the center of their territories during pre-mating, while they defended the periphery and center of their territories equally during post-mating playbacks.

If redstarts normally spend more time in the center of the territory than in the periphery, the observed difference in response could be due to something completely unrelated to the playback experiments. There have been some observations made concerning any normal tendency the redstart may have to remain in either the center or periphery of its territory. The redstarts observed by Hickey (1940) seemed to move back and forth in an indefinite and irregular pattern covering the extent of their territories, and Ficken (1962) has stated that early in the season redstarts "seem to spend no more time at the center than at the periphery" of their territories. The sketch maps of the unmated birds observed in this study (e.g., Figure 1) seem to illustrate this lack of a preference for the center of a territory in the redstart. The locations a bird visited and sang from were distributed evenly between the center and periphery of its maximum territory.

Perhaps the redstarts were more aggressive in the center of their territories

because of previous experience in these areas. Morse (1966) found that the locations of past encounters were an important factor in determining what type of song Yellow Warblers (*Dendroica petechia*) would sing in particular parts of their territories. If the redstart's maximum territory is composed of a number of small areas which will differ in their importance to the bird based upon earlier experience there, the bird's responses to playback in different areas would be dependent upon the history of the bird's relation to its territory. However, it is unlikely that a bird's past experience in a given area was the main reason for the difference in aggressiveness observed in this investigation. The possibility of playing the stimulus tape in a locality of little importance was reduced by selecting areas for playback experiments in which the redstarts had been seen frequently during the one-hour observation periods. Also, the pre-mating playbacks were conducted very early in the season which minimized the effect of past experience on the playback experiments.

The breeding condition of the bird would probably have its effect on territorial behavior. A decrease in territory size might also produce changes in territorial behavior. Huxley (1934) has stated that territories are like "rubber discs"; the more they are compressed, the stronger becomes their resistance against further compression. Furthermore, these two factors may be correlated. All the birds with the largest territories (1.6–2.3 acres) were unmated; four of the five birds with the smallest territories (0.8–1.1 acres) were mated. Of the seven birds whose territory size was known during pre-mating and post-mating, six showed a decrease in size after acquiring a mate (Table 4). Apparently, the size of a redstart's territory is less during post-mating than before a mate is acquired. Although a causal relationship does not necessarily exist, there does appear to be a correlation between territory size and breeding condition. Therefore the effect of these two factors on the redstart's responses to playback could not be separated. In order to define more carefully the role of each of these factors in the redstart's defense of its territory, a larger sample size would be needed with a number of birds in the same stage of the reproductive cycle occupying different sized territories.

During the course of this study each redstart was not observed every day; therefore, the exact date each territory decreased in size could not be determined. It is possible that some of the territories were compressed before the females arrived and in these cases there might not have been any relationship between matedness and territory size. Assuming the territory size would have decreased regardless of the bird's breeding condition the "rubber disc" theory would apply to the redstart's equal defense of its entire territory after this decrease. To determine if this compression of the redstarts' territories

and not their breeding condition was the reason for equal defense in both the center and periphery, a number of birds would have to be continuously observed and the territory size recorded daily.

It appears that the problem of analyzing the redstart's territorial behavior utilizing a playback technique is considerably more complex than initially anticipated. The factors which help to determine this bird's aggressive activities appear to be interacting in a number of ways and are quite difficult to isolate.

The observed shifts in territory size and shape noted in this study appeared to be caused by several factors. The territories of Birds A, B, and C (Figs. 1-2) were reduced at least in part by the addition of late arriving males. In two cases first-year males were able to overcome the aggressiveness of the original territory owner, acquire some of his territory, and obtain a mate. In the only instance where a redstart increased the size of his territory after mating, the location of the female's nest appeared to determine the final size and shape of the territory. Apparently the female has ultimate control over the location of the territory boundaries and if she chooses to nest outside the male's original territory, the male expands his territory to include the area around the new site (Ficken, 1962). In two of the birds there were no noticeable differences in their territory sizes before and after mating. This seemed to be due to the limitations of the area where they first arrived; during pre-mating they were bounded by roads and neighbors on all sides.

The shifting of territorial boundaries in the American Redstart has been observed by other investigators (Sturm, 1945; Ficken, 1962). In this study the upper limit of population density probably was not achieved; denser populations were accommodated by a compression of territories (e.g., the area occupied by three birds during pre-mating (Fig. 1), was supporting five birds during post-mating (Fig. 2)). Several other ways territorial birds might accommodate a denser population are: (a) expand into less suitable habitats, (b) allow the territories to overlap (Weeden, 1965), and (c) increase the vertical foraging range (Ficken, pers. comm.). The redstarts studied here did not appear to utilize any of these other methods.

SUMMARY

Territorial behavior in the American Redstart was investigated by playing a recorded redstart song in the center and on the periphery of a male bird's maximum utilized territory. The bird's responses to the playbacks were observed and analyzed in order to determine what effect breeding condition, size of territory, and location of playback have on territorial defense. One series of experiments was conducted before a male had acquired a mate; a second series was run after a mate had been acquired.

During pre-mating the center was defended more vigorously than the periphery; during post-mating the center and periphery of a territory were defended equally. Some of the factors that might have been interacting to bring about this differential aggression were

discussed with no definite decision reached as to which were the most important; however, there was sufficient evidence to suggest that the redstart's past experience and normal activities were not particularly relevant.

The maximum territory of a redstart appeared to shift in size and shape between the time a male arrived and the end of nest building; usually a decrease in size occurred.

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THE WINTER TERRITORIES OF TUFTED TITMICE

RALPH W. CONDEE

THE winter behavior of Tufted Titmice (*Parus bicolor*) raises many questions. This study attempts to answer three: (1) What area does an individual titmouse cover during its normal winter activities? (2) What relation does the winter area covered by one titmouse bear to that of the other titmice in the general locale? (3) To what extent do titmice associate in flocks with a stable membership, and in flocks of what size?

METHODS

The basis for the answers is the observation of 20 color-banded titmice for varying periods during a seven-month span (1 September 1967 to 1 April 1968). These birds inhabited the southeast slope of Mount Nittany, in Centre County, Pennsylvania, near the town of State College. The study area was 5400 feet long (from southwest to northeast) and 1800 feet wide (from southeast to northwest). The elevation ranged from 1300 feet above sea level (the southeast edge) to about 2000 feet (the ridge of Mount Nittany at the northwest edge). About 20 per cent of the land is open pasture bounded by hedgerows of hawthorn, maple, black walnut, etc.; about 25 per cent is mixed oak forest ranging up to 80 feet in height, with little understory. About 40 per cent of the land, chiefly in a strip along the mountain, is mature deciduous forest—mixed oak, maple, and walnut, with an understory of dogwood, wild grape, etc., unbroken for more than the 5400 feet of the study area, and extending 600 feet down the mountain into the study area. About 15 per cent of the land is cut-over brushy woods, consisting mainly of immature mixed oak, maple, walnut, dogwood, hawthorn, wild grape, bittersweet, etc.

Several techniques and "rules" for locating the titmice were necessary in order to avoid the effect of a feeding station, which might distort the normal winter behavior of the birds. Four (occasionally five) traps operated simultaneously. Each trap was a Potter type, one-, two-, or three-celled, suspended from a tripod made by wiring together three eight-foot metal clothespoles. The traps were baited with about a cup of sunflower seeds (occasionally suet), and pinned open when not in use, thus functioning also, temporarily, as feeding stations.

Every trap was moved to a new location every time it caught a titmouse. The only exceptions were instances where a two- or three-celled trap caught additional titmice before I could return to the trap in my rounds. The purpose of moving the traps in this fashion was to reduce any "feeding-station effect" which might distort the birds' territories. Every trap was moved to another location at least every eight days whether or not it caught a titmouse. Since the traps were pinned open when not in use, they still might entice birds out of their normal territories, even though no birds had been trapped.

All traps were moved at least 100 yards and were not returned to a prior location, or within 100 yards of a prior location, until at least 13 days had elapsed. The eight-day and 13-day periods have no ornithological significance; they simply fit easiest into a pattern of weekend banding. In addition to trap-records, many birds could of course be traced by their color-bands.

RESULTS

Nineteen titmice were trapped and color-banded; in addition one unbanded titmouse avoided the traps late in the study period. The trappings and observations produced 141 place-time records. Of the 19 banded birds, 10 were adults in the autumn of 1967; of these, two were birds banded in the winter of 1965-66, five were banded in the winter of 1966-67, and three were adults first seen in the winter of 1967-68. The basis for distinguishing adults from immatures was mouth-color: light gray upper bill, immature; dark gray, adult (this is based on an unpublished manuscript of Professor Merrill Wood).

In addition to the 10 known to be adults, two birds were of unknown age, being trapped too late in the winter of 1967-68 to have shown immature characteristics. Seven of the 19 were immatures in the autumn of 1967.

Sexing was done by wing-chord measurement (based on an unpublished manuscript of Professor Merrill Wood): 78 mm or less, female; 79-82 mm, unknown; 83 and over, male. Six of these birds were male, five were female, and eight of unknown sex.

In March 1968 the weight of nine birds averaged 22.6 grams (extremes: 20.6, female, to 24.0, one male and one of unknown sex). The 14 titmice of Laskey (1957) in Tennessee averaged 20.5 grams; the 35 titmice of Nice (1933) in Ohio ranged from 20.3 to 25.3 grams.

Figure 1 shows the large patterns of the inter-relations of the titmice. In the study area there apparently were no more than 20 titmice during the period of the investigation: 19 color-banded birds and one unbanded bird seen once, 22 March 1968, at the lower right corner of Area A.

DISCUSSION

The titmice divided themselves into four "clans," designated in Figure 1 as A, B, C, and D. A term such as "clan" seems preferable to "flock" for two reasons: (1) because Gillespie (1930), Van Tyne (1948), and Laskey (1957) observed that the association of titmice during the winter season was a vestige of the family group of the previous season; (2) because an observer seeing a group or "flock" of titmice in certain parts of the area (specifically the overlaps in Figure 1) might be seeing titmice which *normally* group together (a "clan"), or he might be observing a mixed group from two different clans, birds which would soon separate as they moved to other parts of their respective territories.

The composition of each clan was as follows: Clan A—five birds: one male, age unknown; one adult male; one female, age unknown; two adults of unknown sex. Clan B—three birds: one adult male; one immature male; one immature female. Clan C—six birds: one adult male; one adult female; one immature female; three of unknown sex, one of them mature, the other

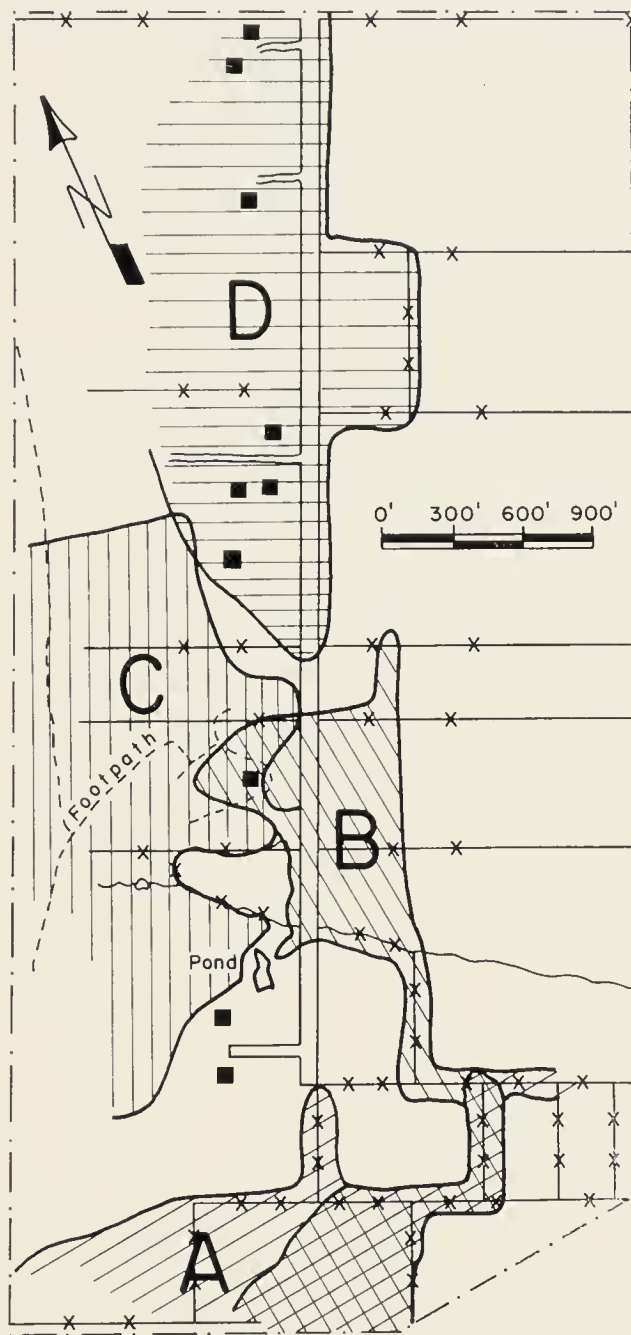


FIG. 1. Winter Territorial Boundaries of 19 Tufted Titmice. Territory A: five birds. B, three birds. C, six birds. D, five birds.

two immature. Clan D—five birds: one adult male; one immature female: three of unknown sex, one of them adult, one immature, and one of unknown age. In addition, as has been pointed out, there was one unbanded titmouse observed on 22 March 1968 in a part of the area visited by both Clans A and B.

Except in one instance, birds of a given clan were never observed outside the territories indicated by the letters A, B, C, and D in Figure 1. The

boundaries in Figure 1 rest on 141 observations and two assumptions: (1) that the territory indicated is the minimum for each clan; (2) that the boundaries of the territory can be determined roughly by drawing lines from one observed point to another along what seem to be the outermost points of the territory. These are not, then, *observed* boundaries; in most instances a titmouse at the territory's "edge"—if indeed it was an edge—flew toward the central area of the territory and not in any path that might be called a perimeter of the territory.

Offutt (1965) reports that "[breeding] territory appeared to extend from about fifteen feet above the ground to the treetops." This does not seem to be true of wintering territory. In winter the titmice associated with their clan at various heights and, except for the areas of overlap, almost invariably stayed away from other territories.

The maximum observed distance covered by any titmouse during the period of observation was approximately 3000 feet; 185, a female of Clan B, banded as an immature on 16 September 1967, was trapped at the northernmost limit of Territory B on 23 September 1967, and at the southernmost limit of Territory B (3000 feet away) on 26 March 1968. In Clan C, 187, of unknown sex, was trapped at the northernmost point in the territory on 29 February 1968, and at the southernmost, 2400 feet away, on 31 March 1968—the maximum distance for a titmouse of this clan. Territory D is at least 2500 feet long (its northernmost limit is known only to the titmice), but I found no one titmouse ranging the whole length of the territory. Nice (1933) writes that her flock of 8 birds ranged over about 20 acres.

Since these observations began well after the end of the breeding season, I can say nothing definite about the relations of the titmice within a clan. Laskey (1957) writes, "My [winter] records . . . indicate that the twosomes may be a mated pair, but not always. They may be birds hatched the previous summer, probably of the same brood, or a parent and a youngster. The small groups may be a family or a brood. I have not seen large groups." This would indicate the internal structure of Clan B as being a male parent with a male and a female offspring. But the internal relations of the other clans are not clear since each has three adults in it.

There are at least two possibilities: (1) that the clans are coalitions of the remnants of several summer families; (2) that the clans are really associations of smaller groups, and that my observations failed to detect the existence of these "septs" within the clans. For example, 794 (an adult of unknown sex) apparently never strayed outside Territory C; but it also never seemed to wander throughout all of C. Its appearances were limited to an east-west strip through the middle of Territory C. 136 (an adult male) ranged through the middle and northern parts of Territory C, but not to the

southern part. On the other hand, 187 (an immature of unknown sex) turned up almost everywhere within Territory C.

Previous banding of titmice (1965–67) at a fixed banding station in this area had resulted in a small number of returns at the end of the breeding season: of the 15 titmice banded between 15 September 1965 and 22 March 1966, only one returned during the winter season of 1966–67. The other 17 birds trapped that winter were previously unbanded.

In 1967–68, scattering the traps and widening the area of observation resulted in the return of three of the titmice from previous years, all of them in Territory A. With the exception of one observation, they never ventured as close as 1200 feet to the feeders and traps they had visited during previous winters. The previous (fixed) banding station had been in the area where (in Figure 1) Territories B and C overlap. One titmouse had appeared three times at this banding station in the spring of 1966, but it never came within 1500 feet of this site in 1967–68. Another bird had appeared 11 times at the banding station during the winter of 1966–67; it appeared there only once (15 March) in the winter of 1967–68. That trip is the only instance of one of these 19 birds moving outside the territorial boundaries of Figure 1 during the winter of 1967–68. A third titmouse had appeared twelve times at the 1966 banding station, but it never appeared in this territory at all in 1967–68. Although it was commonly evident during this period in Territory A, it always remained at least 1200 feet from its previous haunts. A similar phenomenon was noted by Short (1933) and Van Tyne (1948).

With regard to these movements from year to year, Van Tyne suggests that there are two classes of titmice: “*A*, those that remain in restricted home ranges throughout the year (hence repeatedly recorded in a small radius); *B*, those that wander (hence not recorded after banding). It seems reasonable to suppose that the former are fully adult birds; the latter, birds in their first winter wandering widely before settling on a home range.”

On this point A. C. Bent (1946) quoted Dr. Dickey (MS.) who, “referring to Pennsylvania and West Virginia, says, ‘Particularly in autumn and winter, tufted tits are rovers. . . . Bands . . . enter patches of weeds, flit along the courses of streams, cross country roads and highways, and peer forth from cover at farmyards.’ . . . Several other observers have reported winter wanderings of titmice.”

But this does not seem to account for the shift I observed between 1966 and 1968. Take two titmice—165 (adult, sex unknown) and 166 (adult male) as examples: I do not know if 1966–67 was their first winter, but they seem not to have been “wandering.” Together they clocked 23 appearances at the banding station that winter. And their abandonment of their old territory in 1967–68 was almost total, while their adherence to their new territory was

quite close. The record for 017, an adult of unknown sex (banded 17 March 1966) points in the same direction, although there are fewer observations. This behavior looks less like wandering and more like a clearly defined immigration into a new winter territory.

But some titmice are apparently closely attached to a territory from year to year. For example 794, of unknown sex, was trapped in precisely the same spot on 14 October 1965 and 10 February 1968. It was trapped only 300 feet away from this spot on 20 November 1966, 26 April 1967, and 25 February 1968. Some titmice never leave "home," and others apparently shift their base of operations to a nearby area and never, or rarely, return even the short distance of 1200 feet to their previous territory.

My observations markedly disagree with those of Bent's informants. My titmice seemed to move as a group with the same "clan" (family?) and within a defined territory. There was no evidence of "wandering."

Certain clans seemed reluctant to approach each other. The area between A and C produced no records of either clan, and that between C and D produced very few records, although both areas were intensively trapped and observed. On the other hand I did find considerable overlapping in two areas. The point at which B and C overlap (in the center of Figure 1), and A and B overlap (at the bottom of Figure 1) can be described simply as areas with lots and lots of titmice around a great deal of the time. I could see no signs of conflict or territorial clash. It is probably significant that the point where B and C overlap was an excellent area for food—wild grape, hawthorn, bittersweet, oak, etc. And the area was visited by seven titmice: four from Clan C and three from B.

SUMMARY

Nineteen color-banded Tufted Titmice were trapped and observed on a tract 5400 feet by 1800 feet in the seven months from 1 September 1967 to 1 April 1968 in order to observe winter territorial activity. They restricted themselves to four territories with five, three, six, and five birds per territory. The territories seemed to be of irregular shape, making total areas impossible to state. The maximum distance between two points within one territory was 3000 feet. At two points territories were contiguous and few or no titmice were to be found; at two other points territories overlapped and the number of birds was quite high. No conflicts or territorial clashes could be seen. One clan of five titmice included three birds which had occupied another (nearby) territory one or two winters before, but which now remained almost completely outside their previous territories and within their new territory. Adherence to territory was close.

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FOOD HABITS AND FEEDING BEHAVIOR OF THE BALTIMORE ORIOLE IN COSTA RICA

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BALTIMORE Orioles (*Icterus galbula*) are mainly insectivorous during their summer residence in North America (Bent, 1958), but little is known of their food habits while wintering in Central America and northern South America. Slud (1964) mentions that this bird has a varied behavior and diet while in Costa Rica, and A. F. Skutch is reported as saying that Baltimore Orioles subsist on a variety of animal and plant foods (Bent, 1958). However, no qualitative or quantitative data are available concerning the food habits and feeding behavior of this species. In Costa Rica the species occupies a wider range of habitat than do the native orioles and exceeds them in total numbers (Slud, 1964). This study was undertaken to obtain some data concerning the habits of this successful species during its stay in Costa Rica.

MATERIALS AND METHODS

This study was conducted at seven different sites in five of the seven Costa Rican Provinces. Collections were obtained at: Taboga, Guanacaste Province; Heredia, Heredia Province; Turrialba, Cartago Province; and San Isidro, San Jose Province. Observations of feeding behavior were obtained at the collection sites and at three other sites: San Jose, San Jose Province; San Vito, and Rincon, Puntarenas Province. Birds were collected with shotguns at different hours on several dates.

Stomachs from collected specimens were removed as quickly as possible, slit and preserved in a 70 per cent ethanol solution. The number of each item was recorded per stomach and the per cent by volume of each kind of food item was estimated.

RESULTS AND DISCUSSION

Observations of Feeding Times and Activity.—This species frequents borders and boundaries of many types of broken habitats. It is found foraging for food mainly in the canopy, but frequently is found at lower levels. Many times it is found in loose aggregations of birds such as other native and migrant icterids, tanagers, hummingbirds, etc. Associations with particular plants seem to be part of the feeding behavior of the species.

Baltimore Orioles usually become active as soon as it begins to get light in the morning. Within a few minutes of dawn, large numbers of orioles are actively foraging in the canopy layer of the habitats that they are utilizing. Active foraging generally occurs between 06:00 and 08:00. Reduced feeding activity may last until 11:00 or even later, but by 09:00 most Baltimore Orioles have finished feeding and after 11:00 virtually all are resting

TABLE 1
FOOD ITEMS OF SAMPLE 1 (21 STOMACHS) COLLECTED AT TABOGA,
GUANACASTE PROVINCE, COSTA RICA—8-12 FEBRUARY 1968.

Food item	No. of stomachs with item	Mean no. of items per stomach	Mean est. per cent by vol. per stomach
Animal material			
Lepidoptera larvac	17	19	61
Coleoptera	8	1	9
Formicidae	3	2	4
Odonata	3	1	2
Orthoptera	1	0	0
Diptera and larvae	5	0	2
Hemiptera	1	0	0
Insect egg cases	3	0	1
Plant material			
<i>Olyra</i> seeds	2	1	8
<i>Sideroxylon</i> fruit	1	0	1
Unidentified material	18	—	12

somewhere in the shade. On cloudy days the entire sequence seems to be retarded and feeding activity may last later into the morning.

Later a second period of activity occurs, usually beginning about 16:00 and lasting until dark. This feeding period appears to be less intense, as fewer orioles are observed. Those that are observed seem to feed less actively than they did during the early morning period. On cloudy days this second feeding may commence and end early in the day.

Observations of Feeding and Plant Associations.—In northwestern Costa Rica during the early morning active feeding period, large numbers of Baltimore Orioles were observed visiting *Sideroxylon* trees. These trees were flowering and fruiting, but also had heavy foliage. Large numbers of bees, hummingbirds, and warblers were also visiting these trees. As many as 12 to 15 Baltimore Orioles could be observed actively feeding in the tops of these trees, but by 08:30 almost all oriole activity ceased. On one occasion a large group of orioles (8 or 10 birds) was observed foraging in a *Caly-cophyllum candidissimum* tree which had heavy foliage. A few orioles were observed drinking nectar from *Combretum* flowers and foraging in this vine during the early feeding period. After 08:00 and until 11:00 large numbers of orioles visited *Combretum* vines. A few were seen drinking nectar from these vines, but most were either resting or foraging for insects. The most active feeding period, however, seemed to be during the time spent in the *Sideroxylon* trees. During the afternoon period some orioles were observed

TABLE 2

FOOD ITEMS OF SAMPLE 2 (18 STOMACHS) COLLECTED AT TURRIALBA, CARTAGO PROVINCE: HEREDIA, HEREDIA PROVINCE; AND SAN ISIDRO, SAN JOSE PROVINCE—4-8 MARCH 1968.

Food item	Sub-sample A 4-6 March Turrialba (7 stomachs)			Sub-sample B 7 March Cartago (6 stomachs)			Sub-sample C 8 March San Isidro (5 stomachs)		
	No. of stomachs with item	Mean no. of items/stomach	Mean est. per cent vol./stomach	No. of stomachs with item	Mean no. of items/stomach	Mean est. per cent vol./stomach	No. of stomachs with item	Mean no. of items/stomach	Mean est. per cent vol./stomach
Animal material									
Lepidoptera larvae and pupae	5	2	26	6	6	54	3	6	30
Coleoptera & larvae	6	6	44	3	1	4	5	6	46
Hymenoptera	2	1	5	0	0	0	2	1	4
Formicidae	0	0	0	0	0	0	2	1	1
Orthoptera	2	0	10	0	0	0	2	0	2
Diptera & larvae	0	0	0	1	0	5	1	0	0
Hemiptera	1	0	1	0	0	0	2	1	3
Insect egg cases	1	1	1	2	1	7	2	2	6
Araneae	0	0	0	2	1	3	1	0	0
Plant material									
<i>Ficus</i> fruit	0	0	0	2	0	15	0	0	0
Unidentified material	7	-	14	5	-	12	5	-	8

feeding in *Combretum*, *Bursera simaruba*, and *Enterolobium cyclocarpum*; in one instance a few orioles were observed foraging in epiphytic bromeliads. This activity also seemed to be reduced in intensity compared with the early morning feeding in *Sideroxylon* trees.

Observations made in central Costa Rica indicated that Baltimore Orioles foraged for food in trees with bright colored flowers or in trees with heavy foliage. Most Baltimore Orioles in this region were seen during the early morning activity period foraging in *Erythrina poeppigiana* trees which had bright orange flowers and were nearly devoid of leaves. Some Baltimore Orioles were observed in other *Erythrina* spp. and in *Cassia grandis*. A few orioles were observed in *Cordia alliodora* trees which were in flower and had heavy foliage.

In southwestern Costa Rica fewer numbers of Baltimore Orioles were seen. A few orioles were observed foraging in *Cecropia* spp. and *Ficus* sp. which were in fruit. One male was seen eating from a *Cecropia* fruit but spent most

TABLE 3

SUMMARY OF IMPORTANT FOOD ITEMS FOUND IN 38 BALTIMORE ORIOLE STOMACHS
COLLECTED DURING FEBRUARY AND MARCH, 1968 IN COSTA RICA.

Food items	Total number of items	Mean number of items	Mean estimated per cent by volume
Animal material			
Lepidoptera larvae & pupae	482	13	49
Coleoptera and larvae	100	3	19
Other insects and araneae	128	3	12
Plant material	36	1	7
Unidentified material	—	—	12
Total	746	20	99

of his time foraging for insects. One oriole was observed foraging high up in a large *Brosimum utile* tree which was in fruit and had heavy foliage.

Baltimore Orioles observed in the three regions either were seen actively foraging in trees with heavy foliage or were observed in vegetation with bright red or orange-colored flowers such as *Combretum* plants or *E. poeppigiana* trees. Orioles foraging or resting in these plants with brightly colored flowers seemed to be much less active and remained for longer periods of time than those orioles observed in other non-colorful vegetation. Therefore, the possibility exists that these plants not only provide food but also provide a cryptic situation for the brightly colored male Baltimore Oriole.

Stomach Contents Analysis.—Tables 1, 2, and 3 summarize the results of the analyses of stomach contents. It is readily apparent that Lepidoptera larvae and coleopterans make up the most important components of the diet of these winter residents. However, a wide variety of animal species and a few plant fruits were utilized as part of their diets. Lepidoptera larvae appear to be the most important item in the diet of this bird while it is in Costa Rica. Beetles are the next most important part of the diet. However, as sub-sample A and sub-sample C indicate, in Table 2, in some cases beetles may be the most important. This diet information is strikingly similar to the known information concerning the diet of this bird in North America during its summer residence (Martin, Zim, and Nelson, 1951). (Bent, 1958). The similarity of diet between sub-sample A and sub-sample C of sample 2 is interesting. These sub-samples were collected at different locations, on different dates, at different hours of the day and had different sex-age composition; the only equality of the sub-samples was that both sub-samples were obtained from populations of birds utilizing *E. poeppigiana* trees.

No differences in diet between sex and age groups were evident in this study. However, larger samples might show some differences because females and sub-adults seemed to feed over a longer period of time and utilized a wider variety of trees in their feeding behavior than did adult males.

SUMMARY

This study indicates that Baltimore Orioles feed early in the morning and to a lesser degree again in the late afternoon during their stay in Costa Rica. Baltimore Orioles tend to visit certain plants that are either in flower or fruit. Lepidoptera larvae are the most important fraction of this species' diet and coleopterans are the next most important part, the two accounting for about 68 per cent of the total food. A variety of other insects and spiders made up 12 per cent of the diet. Plant material accounts for only 7 per cent of the total diet; 12 percent of the total volume of stomach contents was unidentified but was composed mainly of fragmented insect remains.

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EN ROUTE BEHAVIOR OF HOMING HERRING GULLS AS DETERMINED BY RADIO-TRACKING

WILLIAM E. SOUTHERN

PROBLEMS associated with bird migration, spatial orientation, and navigation have stimulated considerable interest among biologists and others. During the last two or three decades increasing numbers of investigators have studied these problems, and their efforts have been greatly aided by the introduction of new sophisticated equipment and techniques. One of these recent approaches has been the application of radio-tracking equipment. This paper is the result of one attempt to use such equipment.

Prior to the availability of telemetry equipment, experimental birds were only observable at release times, possibly for a short period thereafter, and occasionally upon return. Seldom was it possible to determine the actual routes taken by homing birds or their apparent responses to environmental clues while en route. Exceptions to this statement are Griffin's and Hock's (1949) airplane tracking of Herring Gulls (*Larus argentatus*) and Gannets (*Morus bassanus*) and Hitchcock's (1952) and Griffin's (1952) airplane observations of pigeons (*Columba livia*). These data, however, were insufficient to indicate the procedures involved in avian homing.

During the summers of 1963 and 1964, I conducted orientation experiments with 50 adult Herring Gulls, 323 adult and subadult Ring-billed Gulls (*L. delawarensis*), 56 juvenile Ring-billed Gulls, and 294 Ring-billed Gull chicks from a colony near Rogers City (Presque Isle County), Michigan. My objectives were: (1) to examine the orientation requirements of each species; (2) to evaluate the homing and orientation abilities of both species; and (3) to determine the behavioral mechanisms and environmental factors associated with orientation as performed by these species.

METHODS

Adult Herring Gulls were captured with nylon snares, color-marked with alcohol soluble biological stains, and subjected to typical homing trials. During 1964, the gulls were anesthetized with Equitol (4.5 ml/kg) and transported to release sites in burlap bags. This paper pertains to one aspect of the study, the behavior of 41 Herring Gulls that were radio-tracked during homing flights from release sites located up to 110 miles from the colony (Table 1). Tracking distances for individual gulls ranged from 3 to 138 miles. Seven other gulls were equipped with transmitters but they were not tracked more than one mile because of transmitter failure, signal interference, or undetermined factors. The results discussed at this time are based on a total 1307 miles of radio-tracking and at least 285 radio-contact hours with experimental birds.

The radio-tracking equipment used during this study and some of the problems associated with the field application of this technique have been discussed previously (Southern, 1963, 1967). Two mobile units were used and each vehicle was manned by at least two

TABLE 1
SUMMARY OF RELEASE SITES AND SUCCESS RATES FOR RADIO-TRACKED HERRING GULLS.

	Distance of Release Sites from Colony							
	10 miles	20 miles	30 miles	40 miles	50 miles	60 miles	80 miles	110 miles
No. tracked	5	14	4	4	4	3	4	3
No. returned	5	8	4	3	3	2	2	2

41 tracked; 29 returned; success rate 70.8 per cent.

persons, a driver-receiver operator, and a recorder-map reader. One permanent station antenna was also maintained.

Twenty-nine (70.8 per cent) radio-tracked Herring Gulls returned successfully (Table 1) in periods ranging from 40 minutes (10 miles to release site) to 151 hours (30 miles). Eighteen of the 29 successful gulls were tracked during all, or most of their journey. The other returning individuals, and also those failing to home were tracked for periods ranging up to five hours. Their complete flights were not tracked for several reasons, e.g.: (1) a lack of adequate roads for use by tracking vehicles; (2) several gulls landed and remained at the same location for several hours and radio contact was eventually discontinued because of operator fatigue or other obligations; (3) prolonged flights by gulls in directions other than homeward resulted in the cessation of tracking operations; and (4) transmitter signals were lost as a result of human error, environmental factors, or equipment malfunction. Although several gulls were tracked over meandering routes of 100 or more miles, the farthest release site from which a gull's entire homing flight was tracked was 60 miles.

No attempt was made to initiate long-range trials since considerable information was available for Herring Gulls (Griffin, 1943; Matthews, 1952). I decided that the shorter trials, up to about 150 miles outside of the normal feeding range, would provide considerable data regarding the necessary environmental clues, homing success rates, and general orientation behavior. Results from such trials should also provide some information regarding the factors associated with orientation during longer flights by this species. Results from various studies tend to substantiate this contention (Kramer, 1961). Regardless of the type of homing study conducted, the conclusions which are drawn must always be restated in terms applicable to bird migration.

RESULTS

Flight patterns of successful homers.—Twelve (66.6 per cent) of the 18 Herring Gulls that were tracked for significant distances pursued south, east, or southeast courses during early flight periods, i.e., after initial departure. The other six gulls selected north (two), west (two), northeast (one), or southwest (one) as preliminary headings. The selected departure direction was often followed for a half mile or more before a change was made. In most cases (89 per cent), the initial heading was followed for about one-half mile and then it was altered by erratic or zigzag flight, with a half mile or less being flown in each of a variety of directions. In a few instances, a par-

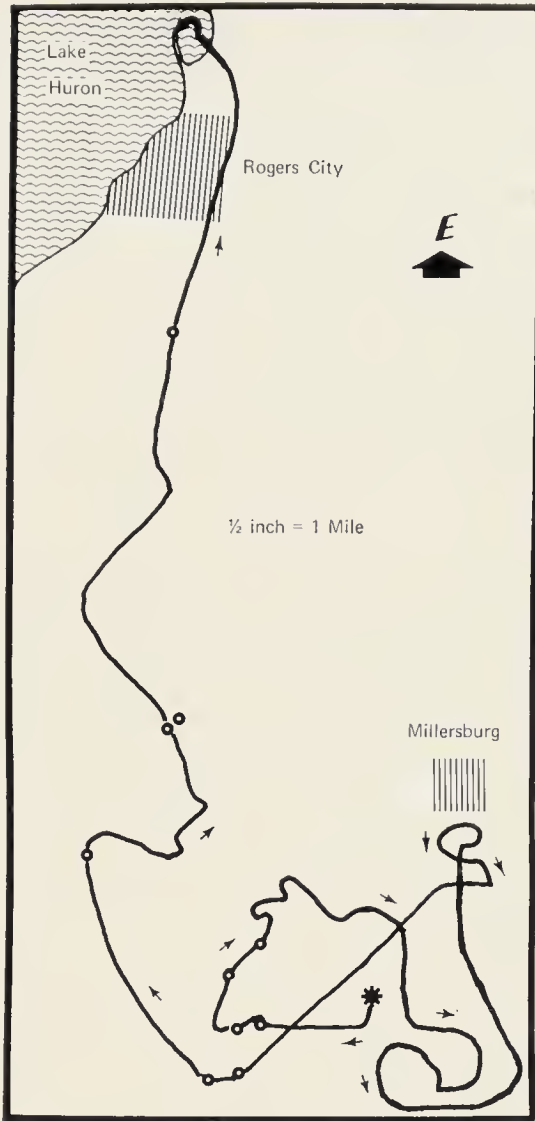


FIG. 1. Exemplary route of a radio-tracked Herring Gull released about 20 miles west of the colony. The colony is located on the peninsula east of Rogers City. Key to symbols: * = release site; o = period of circling behavior; → = direction of flight.

ticular route was maintained for about two miles before a different heading was selected. The fluctuating flight patterns involved as few as four headings and as many as 14. Repetition of easterly or southerly courses was common during prolonged periods of zigzag flight. Such behavior was occasionally interrupted by one or more circles that varied in diameter from a few yards to over one-half mile. The flight path of a Herring Gull tracked from its release site 20 miles west of the colony is illustrated in Figure 1. It is presented as a typical example of the type of information that was recorded for each homing flight.

The circling and erratic patterns were often followed by periods of straight flight which lasted for perhaps several miles. Ten (45.4 per cent) of the 22

Herring Gulls released between 10 and 30 miles west of the colony followed a course leading to some point on Lake Huron, usually Hammond Bay, which was located north of the colony and represented the nearest large body of water. Two of these gulls returned home promptly—in 40 and 50 minutes—from this point by routes over the water, but within one-half mile of the shoreline. The other eight birds spent extended periods of time on the water and occasionally made additional exploratory flights. These gulls required from 3 to 36 hours (average 17 hours) to return. A few individuals failed to return from this location and one gull, that was released 20 miles west of the colony, homed successfully without deviating its course toward Hammond Bay. It departed eastward, and pursued a fairly direct route to the colony after performing a few circles and zigzags. The entire flight required 50 minutes.

Twelve of the 22 Herring Gulls released up to 30 miles west of the colony departed along north, west, northwest, or northeast routes. Seven of the 12 returned in periods ranging from 3 to 151 hours (average 52 hours). Two gulls pursued northward courses toward a large inland lake (Black Lake) near Onaway. Both birds landed and remained on the lake for significantly long periods. Their courses between Black Lake and home were not determined, but one had a homing time of 85 hours, and the other 151 hours. In these instances, it seems that "incorrect" initial headings resulted in greatly increased average homing rates.

Individuals released at more distant sites, up to 110 miles, performed similarly with respect to general flight behavior. Only one Herring Gull was tracked during its complete homing flight from a site 60 miles from home. This bird was released near Little Traverse Bay (Emmet County) on Lake Michigan and spent six hours on the water preening, bathing, and just sitting. Thereafter, it flew southeast, zigzagged, circled, and then resumed a southeast course. This route was altered later and the gull followed a fairly direct path eastward to the colony. The flight lasted approximately two hours. Each gull released at locations along the other Great Lakes, or large inland lakes, reacted positively to these features and usually landed on the water. One of these birds returned from Lake Superior (110 miles from home) after I discontinued tracking operations following a three hour wait for its departure. It returned 21 hours later. A Herring Gull released 105 miles north-northwest, but inland from Lake Superior, followed an erratic course, changing directions 14 times in 12 minutes. Its flight path was not tracked for more than 20 minutes because roads were unavailable. This bird required 125 hours to return.

Gulls that successfully homed from distant locations exhibited the behavior patterns discussed in this section, but such activities were not unique to

successful individuals. Gulls that proved to be unsuccessful also zigzagged, circled, and altered their flight in other ways. There were, however, a few differences in flight patterns of the two groups and these will be discussed after I have described the remaining two categories.

Flight behavior of homing failures.—Six Herring Gulls failed to return from distances ranging up to only 30 miles from the colony. These individuals were tracked for distances totaling 170 miles and contact was maintained for about 45 hours. Only one of the six gulls departed on a southeasterly course. After circling and changing headings numerous times, it flew north-northeast to Hammond Bay. Its particular course headings were followed for various distances (e.g., 0.5, 1.0, 4.0, and 7.0 miles). One other gull from this group was tracked to Hammond Bay, but its original departure flight of 0.5 miles to the north was followed by turns to the east for 3 miles, north 10 miles, and finally northeast 4 miles to the Bay. It landed on the water, remained for a short time, and later flew parallel to the shoreline for about two miles toward the colony; however, it never returned. It seems unlikely that these two individuals would get this close to home and then be unable to find their way over the remaining distance. It is more likely that the gulls failed for other reasons, possibly because of a motivation loss (i.e., tendency change) which resulted from handling procedures during preparation for release. It is also possible, although unlikely, that both transmitters ceased to function after I left the birds at the above mentioned location and, as a result, I was unable to record their return.

The other homing failures in this distance category departed to the north, west, or northeast. One of these was tracked for 18 miles, to within seven miles of the colony, before contact was lost. The apparent failure of this bird to return might also be explained by one of the possibilities given previously, rather than by disorientation. The cause for loss of radio-contact was not determined.

There were six homing failures from distances ranging from 40 to 110 miles. Each individual circled and zigzagged soon after departure from release sites and two headed in homeward directions. The six gulls were tracked for 227 miles and for periods totaling 38 hours. In general, their behavior was comparable to that of birds failing to return from shorter distances.

Activities of delayed homers.—This discussion is not really distinct from the previous two topics. The behaviors described herein were also performed by members of the successful and unsuccessful groups.

Answers to several of the questions that continually recur during homing experiments may result from a knowledge of the activities and whereabouts of the birds that required, or took, unusually long periods of time to return from trials. Radio-tracking procedures enabled me to determine some pre-

liminary answers to these questions even though I was unable to continually follow all gulls that were equipped with transmitters. Three factors usually contributed to slow homing rates and to periods of extended absence: (1) extensive flights in non-homeward directions; (2) long periods spent in other than flight activity; and (3) hesitancy to enter the colony or increased wariness of the experimenter after return.

Several individuals were tracked for significant distances, up to 100 miles, in other than homeward directions. These flights might represent attempts to search for the familiar area or landmarks associated therewith, or they may be indicative of disorientation. The types of circling and zigzag patterns described previously were often repeated during such flights. These behaviors resembled the theoretical search patterns described by Griffin (1955). Searching, as recorded by radio-tracking, is not, however, as regular in pattern or as consistent in occurrence as those diagrammed by Griffin. It is interesting that many gulls eventually homed after flights of this nature; however, the factors associated with their eventual ability, or desire, to return were not determined. Radio-tracking data showed, at least in a few cases, that the eventual homeward flights were not direct, but usually involved zigzag patterns.

At least nine radio-tracked Herring Gulls landed in fields or on lakes and remained there for fairly long periods. Several untracked individuals behaved similarly. Occasionally these landings occurred immediately after release, particularly when gulls were freed near lakes or at night; but, on other occasions, the birds landed after traveling 15 or 20 miles. Recorded duration of such "rest periods" ranged from 15 minutes to 6 hours. It is possible that particular individuals remained even longer in one place since I usually discontinued tracking operations after the experimental subject remained at one location for three hours. "Rest sites" varied from lakes to open fields near release sites to similar areas located adjacent to the colony. Herring Gulls tracked along the south side of Lake Superior appeared attracted to flocks of local Herring Gulls whereas Herring Gulls released closer to home and Ring-billed Gulls released at all sites failed to show comparable tendencies. Several Herring Gulls spent at least three hours with these local groups of Lake Superior Gulls. There was no indication that this social attraction had any influence on orientation success. Gulls known to associate with local flocks required from 24 to 125 hours to return from a site 110 miles away.

The increased wariness of some individuals was mentioned earlier. Radio-tracking results showed that particular gulls spent several hours on the water or feeding near the colony prior to their actual return. Other birds returned, but were extremely nervous and departed when the observers approached.

Awareness of this type of behavior creates some concern regarding the accuracy of figures denoting homing success of non-tracked subjects used in this study and others.

Comparison between en route behaviors of successful and unsuccessful Herring Gulls.—There were no obvious differences, of apparent significance, between en route flight behavior of successful and unsuccessful Herring Gulls. Both groups performed periodic circling and zigzag patterns which were interspersed with straight flights ranging up to 10 miles in length. A variety of temporary course headings (4 to 14) were followed by particular individuals of each group. Gulls released adjacent to large bodies of water usually landed. Birds that encountered lakes or open fields after departure from release sites also landed occasionally.

A few behavioral variations were apparent. The primary difference existed in departure directions. Approximately 68 per cent of the successful Herring Gulls departed to the east, south, or southeast which often represented the homeward direction. In contrast, only 25 per cent of the Herring Gulls that failed to return selected one of these three directions. This might seem to suggest that departure directions are indicative of homing ability; however, observational data failed to support this possibility. The other apparent behavioral difference pertained to the relative amounts of zigzagging. Successful gulls zigzagged less during homing flights. Several directions were pursued for various distances by the successful birds but the routine was not repeated as often nor did they pursue the number of different headings recorded for unsuccessful gulls. Several unsuccessful birds zigzagged for longer periods and performed this behavior in a much less regular fashion than did successful gulls. The homing failures sometimes changed course headings frequently, maintained new headings for shorter periods, and were likely to repeat these directions during the same zigzag sequence. The general impression was that of disorientation, or at least difficulty in selecting or maintaining a preferred course.

RESPONSE TO TOPOGRAPHICAL FEATURES

It is extremely difficult to evaluate accurately the role of landmarks in avian orientation. It appears almost impossible to determine by currently available techniques whether or not a bird is responding to specific topographic features. It is equally difficult to measure the extent of what might be considered a positive response to landmarks under field conditions. Regardless of this, many authors have reported various effects of landmarks (e.g., mountains, large bodies of water, valleys, shorelines) on homing birds. Matthews (1951, 1953, 1955) thought such features were used in landmark orientation; Graue and Pratt (1959), Hitchcock (1952, 1955),

Pratt and Thouless (1955), and Pratt and Wallraff (1958) believed they served as distracting factors; and others, Griffin (1952), Hitchcock (*op.cit.*), Arnould-Taylor and Malewski (1955), and Kramer (1957), have credited such features with having a type of funneling effect on birds. Schmidt-Koenig (1965), however, has pointed out that a good deal of evidence speaks against the role of landmarks in each of these three apparent responses. He feels that landmarks are certainly involved in recognition of home areas.

During this study it was occasionally possible to record the apparent reactions of gulls to particular gross land features (e.g., large bodies of water). If an experimental bird altered its course in accordance with particular landforms, this was considered as a positive response to that factor and that it is possibly involved in orientation.

Although radio-tracking techniques enabled me to determine the approximate route taken by homing birds, the method is not refined enough to accurately pinpoint a gull's position with relation to particular land features. The usual degree of plotting error encountered during triangulation on a transmitter-bearing gull's position would place the bird within a three- to six-acre area at a tracking range of about two miles. This error is further increased by the use of mobile units since the exact position of the vehicle cannot be determined. As tracking ranges decrease, as with landed birds or those meandering in one area for some time, tracking accuracy significantly increases. Even with maximum tracking efficiency, it is impossible to know the range of a bird's vision and to even postulate on the location of potential clues within the range of vision.

Because of these difficulties and others, it is obvious that no thorough evaluation of terrestrial clues has been conducted to date. Hochbaum's (1955) outstanding interpretation of waterfowl behavior probably represents the most thorough attempt. Until we possess a better understanding of avian learning, memory, and responses to particular land features, I consider it impossible to disregard the potential for birds using such features in long and short distance orientation.

In spite of these handicaps, it was possible to determine the reactions of radio-tracked Herring Gulls and color-marked Ring-billed Gulls to several types of gross land features. These were: (1) shorelines of the Great Lakes; (2) river valleys; (3) wooded moraines; and (4) roadways. More evidence was obtained regarding responses to shorelines since these features were most extensive and because it was easier to determine the bird's course in relation to these features.

A total of 69 gulls were released along the Great Lakes during the two years. Thirty-eight (55.1 per cent) returned successfully (Table 2). Seven of the Herring Gulls were radio-tracked for a total of 390 miles. Without

TABLE 2
RESULTS OF HOMING TRIALS ASSOCIATED WITH THE GREAT LAKES.

Lake	Number released	Distance (miles)	Failed	Returned	Success per cent	Time range (hours)	Average
Michigan	13	68-82	7	6	46.2	16-29	26.2
Straits of Mackinac	8	55-60	1	7	87.5	7-28	20.1
Huron	17	15-17	9	8	47.1	2-88	38.5
Superior	31	85-150	14	17	54.8	19-92	43.1

exception, gulls released near one of the lakes followed the shoreline. In every case where the shoreline approximated a north-south direction and release sites were over 20 miles from home, a majority (78 per cent) of the gulls departed northward along the shore, regardless of homeward direction. Over half (56.8 per cent) of these birds failed to return. Gulls released at two localities, Lake Michigan (near Cross Village, Emmet County) and Lake Superior (north shore near Montreal River, Ontario), were all unsuccessful.

The activity of individuals released along the Lakes involved "resting" on the water but also periods of flight paralleling the shoreline. In many instances, these routes lead gulls farther from home. After I made several releases at particular sites, it was often possible to predict the outcome of the trials; i.e., most gulls departed northward along the shore and apparently required long periods to return or failed to return. Tracking records and observations of ring-bills suggested that they followed the shoreline in an attempt to locate familiar landmarks. The shoreline, although probably not visited previously by these individuals, resembled the home area and the typical situation a gull would normally frequent. The typical response to this situation was not suggestive of any ability to navigate or orientate by means of the sun or physical clues. The shoreline courses were followed for considerable distances in some cases and possibly until the desire to home was lost. It is also possible that these responses represent an attempt to select air currents suitable for flight. Updrafts would probably be associated with the Great Lakes shorelines and some moraines, and rising warm air from paved highways might effect low level flights. Therefore, response to these features might be related to flight dynamics and not to homeward orientation.

Two Herring Gulls released inland were tracked while they were apparently following the meandering course of the Ocqueoc River (Presque Isle County). Both birds followed the irregular non-homeward course of the river for about four miles. Thereafter, they headed on a more direct homeward course.

The river may have provided the necessary clues for selection of the latter course.

Only circumstantial evidence exists to support the speculation that Herring Gulls responded to moraines or highways. One individual was definitely observed to change its course to correspond with a north-south terminal moraine located about nine miles west of the colony. The west side of the forested hill was followed south for two miles before the gull angled eastward toward home. Several individuals appeared to follow roads during periods of low flight. They flew straight courses over the highway at elevations of 100 to about 200 feet and for distances ranging up to nine miles. While it seems unlikely that gulls could use individual roads as orientational clues outside of their familiar area, it is possible that the overall pattern of highways observable at high altitudes might influence flight direction during homing trials. Hochbaum (1955) referred to the use of various types of topographical features by waterfowl during flights within the familiar area. He also indicated the apparent use of similar clues during migration and showed that topographic configuration of the earth's surface channels flight in some areas. Further supportive evidence for use of landmarks was provided by Dorst (1963), Griffin (1952), (1955), Tinbergen (1949), and Wilkinson (1952). Griffin and Wilkinson have also demonstrated that these clues could be used in association with purely random search patterns. Skinner's (1950) work has provided additional support to this possibility by showing that the visual perception of pigeons is highly developed and would permit use of such clues. Skinner also found that pigeons possess visual memory and are able to respond to specific visual stimuli four years after the initial tests. Hamilton (1962), however, has suggested that these observations in themselves do not give evidence that features of the terrain establish the basic course of flight but only that passing birds respond to topography.

In general, it appears that a strong case still exists for landmark orientation by some species. However, so long as we must attempt to guess at what the bird might be seeing, recognizing, and responding to while en route, it will be impossible to adequately evaluate the role of topographical features in avian orientation.

SUMMARY

Forty-one Herring Gulls were radio-tracked during homing trials. Twenty-nine radio-tracked gulls returned successfully, 18 of which were tracked during essentially all of their flight. Initial flight behaviors were classified as direct, delayed, and those involving "rest periods." The flight patterns of successful, unsuccessful, and delayed homers are discussed.

Three factors contributed to slow homing rates: (1) flights in non-homeward directions;

(2) long periods involving other than flight behavior; and (3) hesitancy to actually enter the colony upon return.

Flight patterns of homing birds resembled the theoretical search patterns described in the literature. There were apparent responses in relation to particular topographical features, some of which could be predicted in advance by observers. Gulls followed shorelines of lakes, a river basin on one occasion, and a terminal moraine. Landmarks apparently influenced the direction of Herring Gull flight and may have played a role in orientation.

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NEW LIFE MEMBER

A recent addition to the roster of Life Members of the Wilson Ornithological Society is Dr. Richard C. Banks of Alexandria, Virginia. Dr. Banks, who holds degrees from The Ohio State University and the University of California, Berkeley, is currently Chief of the Bird Section, Bird and Mammal Laboratories, Division of Wildlife Research, Bureau of Sport Fisheries and Wildlife. His ornithological interests are in the systematics of North American birds, hybridization, and the biology of introduced birds, and he has published about 60 papers on birds and mammals. He is currently the Secretary of the A.O.U. and is also a member of the Cooper Society, the American Society of Mammalogists, Society of Systematic Zoology, and the Biological Society of Washington. Dr. Banks is married and has two children.

MOLT AND TAXONOMY OF RED-BREASTED NUTHATCHES

RICHARD C. BANKS

ROUTINE identification of a small series of Red-breasted Nuthatches (*Sitta canadensis*) at the U. S. National Museum necessitated a review of the recently proposed (Burleigh, 1960) division of that species into two subspecies, *S. c. canadensis* in eastern North America and *S. c. clariterga* in the west. Most authors who have dealt with the species recently have not used the trinomials and have not commented on the recognition of geographic variation in this species (e.g., Mengel, 1965; Johnson, 1965; Godfrey, 1966). However, Todd (1963:533) commented that the proposed form "does not appear to me to be sufficiently well characterized," and Phillips, Marshall, and Monson (1964:114) stated that "careful examination of recent fresh fall skins from Maine and Arizona fails to reveal racial differences. . . ." Bailey and Niedrach (1965:582) used the name *clariterga* without taxonomic comment.

Despite the consensus that the race *clariterga* is not valid, it seemed advisable to review the material on which its proposal was based. Burleigh (1960:212) stated that *S. c. clariterga* differed from nominate *canadensis* by having the "upperparts lighter and more bluish and lacking to a large extent the grayish wash characteristic of the nominate race." In a preliminary examination of subspecifically identified material at the U. S. National Museum, the characteristics of the two groups of specimens as outlined by Burleigh (1960) were plainly evident to me. However, I was disturbed by the large number of eastern specimens that had been designated as members of the western race, and vice versa; the proportion seemed too high even for such an erratic wanderer as the Red-breasted Nuthatch. A more detailed study convinced me that the racial division should not be recognized. More importantly, I believe, reassessment of the evidence has made it possible to state rather precisely how it was misleading and why the name *clariterga* must be considered a synonym of *canadensis*. This could not have been accomplished without examination of the material used in the original study. The conclusions based on the study of the material in the U. S. National Museum were checked and verified by examination of the large series of *Sitta canadensis* at the American Museum of Natural History.

MOLT AND AGE CHARACTERS

To determine whether variation related to age might either mask or enhance any trends of geographic variation in color, I studied specimens in the complete late summer molt in an attempt to develop criteria for the separation of

age groups. Even though no such criteria were found, a brief discussion of this phase of the study is a necessary prelude to a consideration of the basic problem.

Ageing.—The plumage of juvenile Red-breasted Nuthatches is extremely similar to that of adults. The similarity is enhanced by the structure of the feathers of adults, which, with their widely spaced barbs, have the soft appearance usually associated with juvenile birds of passerine species. The difference in structure between the adult and juvenal body feathers is most noticeable on the ventral surface, but since this area is among the first to undergo molt, the distinction is soon lost. Juvenile males have dull rather than shiny black caps, but this distinction also is soon lost because of the rapid progress of molt. Young females have a duller gray pileum than adults, without black feather edgings, but the presence of the latter is highly variable even in adults.

Birds which are involved in the postnuptial or postjuvenal molts can be aged as first-year or adult by the fact that only adults molt the flight feathers. This distinction can be made through virtually the entire period of molt, since the inner primaries of adults are among the first feathers to be lost and the outer primaries are among the last to complete growth. In the final stages of molt, when the primaries of adults have all regrown, the relatively older remiges of the juveniles are more worn than those of adults, but I have been unable to use this feature consistently or with confidence to age specimens. I have not found any differences of shape or color between the juvenile and adult flight feathers or coverts which might be used to separate age groups, and there seems to be no way to distinguish adult birds from first-year birds after the assumption of the adult or first basic plumage.

Molt in adults.—The complete postnuptial (prebasic) molt of adults may begin as early as the middle of June. Molt of the primaries begins slightly before molt of the body feathers, but replacement of the latter proceeds rapidly and the change of plumage in the two areas is completed more or less simultaneously. Molting adults in the collections studied were too few and variation too great to permit statements of precise correlation between primary and body feather molt, but most stages of primary molt were represented and a few generalizations can be made. Fewer females than males were available and the comments presented here are based mainly on the males, but there seems to be no essential difference between the sexes either in timing or progress of the complete molt.

At the time that the first or second primaries are in sheath there is no or very slight molt of the body feathers; at most a few new feathers may be coming in on the lower throat and upper breast. Even by the time that primary 6 is partly grown, the body molt may be restricted to a small area of the upper

or central breast, but usually by this time extensive feather replacement is occurring on the throat and breast, extending slightly down the flanks. Also at this stage molt is in progress on the upper back and on the anterior part of the crown. When primary 7 is in sheath, body molt has extended farther down the flanks and there are some new feathers on the upper and middle part of the back. Most of the anterior crown is new, and there are many feathers in sheath on the posterior crown and on the forehead. Molt of the ventral surface, except the lower flanks, may be nearly completed by the time primary 9 is in sheath, before primary 10 is lost, but even when this outermost primary is missing there may be many sheaths on the lower throat. At the latter stages the back will contain a mixture of old and new feathers with some in sheaths, and the crown will have many sheaths posteriorly. In birds, marked adult by collectors, in which all primaries have been replaced, all the body feathers are also new.

There is considerable variation between individuals in the timing of the annual molt. For example, birds with primary 5 in sheath were taken as early as 3 July and as late as 3 August. Individuals with primary 6 in sheath were taken on 24 June and 11 August. A bird with primary 9 in sheath was taken 27 August, whereas one with primary 10 in sheath was taken 27 July. These comparisons point up the fact that birds of a given date may be as much as 6 weeks, perhaps more, apart in plumage stage (or feather age). It is important to keep this in mind if one wishes to compare individuals or series in strictly comparable plumage.

Molt in juveniles.—The postjuvinal (first prebasic) molt of the body feathers of young nuthatches begins more or less simultaneously in several areas of the body. Sheaths appear early on the central throat and the upper breast, and at about the same time on the central crown and lower back. On the ventral surface, the area of new feather growth expands to the lower throat and central breast, and includes the upper part of the flanks. During this stage replacement of feathers dorsally expands to take in the entire crown. In a slightly later stage, when on the ventral surface many new feathers are showing through the old ones, molt is extensive on the throat and breast, extending posteriorly to the central flanks. Also at this time it is extensive on the crown and hindneck, and there are some sheaths on the central back. Molt progresses rapidly from this stage, with the entire body soon showing more new feathers than old. There is no replacement of flight feathers in this molt.

As in adults, there is a high degree of variability in the timing of the onset and completion of the molt. Birds in the very earliest stages of body molt have been taken as early as 12, 13, and 18 July, and as late as 16 September. Similarly, birds in the very latest stages of molt, or which have just completed the

molt, are available from 29 and 30 July, and from 22 and 24 September. This again points out that similar plumage stages may be as much as two months apart chronologically.

THE SUBSPECIFIC DISTINCTION

Birds taken in the months of November and December were sorted geographically, and eastern specimens were compared to western ones. Although the difference in color of the dorsal surface reported by Burleigh (1960) was evident, approximately 15 per cent of the birds fell into the "wrong" group when the birds were arranged by color and geography. The same situation held when birds from January and February were compared, or when samples from any relatively discrete time period were studied.

As noted earlier, however, birds taken in a given time period may differ by as much as 2 months in the age of the plumage; that is, one bird may have a feather coat that has been subject to 2 months more wear than another bird taken at the same time. To avoid comparing birds of different plumage ages, I selected birds that had just completed, or were just completing, the annual molt. When eastern and western examples of similar molt stages, or of similar plumage ages, were compared, no differences in color could be noted. Thus it appears that the wear that can take place during a period of approximately 2 months was at least in part responsible for the color difference that had been attributed to geographic variation. Once the color variation in specimens of similar collection date was noted, it was reasonable, although erroneous, to ascribe it to geographic factors because of the additional factors discussed below.

When I sorted birds taken in a particular month according to the subspecific names *canadensis* and *clariterga* that had previously been put on the labels, several of the former seemed at first to fit better with the series of lighter, bluer birds called *clariterga*. In every instance, however, closer examination refuted the first impression. Several of my colleagues at the U. S. National Museum were asked to examine the series, and each of them picked some or all of the same birds from the darker group for more critical comparison with the lighter group. On close comparison, however, none of those selected quite fit into the series called *clariterga*; all were too dark. It became evident that the birds selected were those in fresher, less worn plumage. Finally it was noted that the white superciliary stripes of these specimens showed considerable sooting, a condition that was present but not evident on other parts of the dorsal surface because of the general blue-gray color of the birds. More of the eastern birds were sooted, and thus darker, than western ones, presumably because of the greater degree of industrialization in the eastern part of North

America, which is thus a second factor to be considered in the apparent geographic variation.

Another determinant of the appearance of a color difference between eastern and western birds was the quality of the prepared skin. Not only were the supposed *canadensis* chosen for comparison with *clariterga* in fresh but sooted plumage, but they were also well prepared specimens, with the dorsal feathers very neatly arranged. It turned out that most of these selected eastern specimens had been collected by Burleigh. A result of the exceptional quality of Burleigh's specimens was that they were not strictly comparable to the main body of material in the collection. Because of his extensive work in the western portions of the United States there was a preponderance of better quality material from that part of the country in the U. S. National Museum for comparison with relatively poorly prepared material from the east.

SUMMARY

The postnuptial and postjuvinal molts of Red-breasted Nuthatches occur from middle June to late September. Some birds may be nearly finished with the complete molt before other individuals begin, so that specimens taken at any given time may differ by as much as two months in the age of their plumage. No characters useful in ageing birds after the completion of the autumn molt were found.

The proposed racial subdivision of *Sitta canadensis* was based on misleading evidence resulting from variation of plumage age in birds assumed to be seasonally comparable, sooting of birds in industrialized parts of the country, and variation in quality of prepared specimens.

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A COMPARATIVE STUDY OF THE FOODS OF THE SORA AND VIRGINIA RAIL¹

GERALD J. HORAK

THREE species of rails nest regularly in the marshes of northern Iowa: Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*), and King Rails (*Rallus elegans*). The former two are quite abundant in most years and usually frequent the same habitat. To compare their possible competition for foods, a study was conducted during the summers of 1963 and 1964. Emphasis was placed on comparing food availability with its utilization by the two species of rails. Attempts to correlate food habits with food availability have been reported by Glading, Biswell, and Smith (1940) in their study of California Quail, by Bellrose and Anderson (1940) on ducks, and by Hungerford (1957) on Ruffed Grouse. The present study attempts to show this relationship for the Sora and Virginia Rail.

STUDY AREA

Rails were collected from three areas in Iowa: Jemmerson Slough in Dickson County (Section 31, Spirit Lake Township); Goose Lake in Hamilton County (Section 27, Lyon Township); and Smith's Slough in Clay County (Section 26, Lake Township). Most of the work was conducted on Smith's Slough, a 287 acre marsh bounded by Trumbull Lake on the west, cultivated land on the north and south, and by county road H on the east. Water leaves this study area from the southwestern section by way of two narrow channels which lead into Trumbull Lake. The marsh is never more than 4 feet deep and most is less than 2 feet in depth.

The dominant vegetation of the upland area surrounding Smith's slough is Kentucky blue grass (*Poa pratensis*). The wet-meadow and shallow marsh areas consist mainly of slough grass (*Spartina pectinata*), sedge (*Carex* spp.), and smartweed (*Polygonum* sp.) The major plants of the deep-marsh zone are narrow-leaved cattail (*Typha angustifolia*) and river bulrush (*Scirpus fluviatilis*). Approximately 25 percent of the deep water part of the marsh was open water during the study.

METHODS

Analysis of food habits.—Rails were collected either by shooting or by driving them into traps. The gizzard and proventriculus were removed as soon as possible and preserved. The preserved organs were cut open and the contents were washed into a sieve constructed of three strainers: a $\frac{1}{16}$ -inch wire mesh, a $\frac{1}{32}$ -inch wire mesh, and a linen cloth to catch the finer particles. If the gizzard contained grit, the sample was placed into a 250 ml beaker and carbon tetrachloride was added. After a few minutes, the grit sank to the bottom and the food material floated. The food and grit were placed in individual Petri dishes and allowed to dry for several hours.

The contents of the organs were then examined with a dissecting microscope. The sample was separated into major groups and an estimate was made of the numbers

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of each type of food. Seeds were identified with the aid of Martin and Barkley (1961), and Isely and Braggonier (1962); and invertebrates with the aid of Eddy and Hodson (1958), Pennak (1953), and Usinger (1956). After all the gizzards were examined, the process was repeated and the contents were rechecked without reference to original identifications. This time the sample was measured on a volumetric basis along with the enumeration. Each major group of foods was dried and placed in a graduated centrifuge tube which measured to the nearest $\frac{1}{10}$ ml. Particles smaller than $\frac{1}{10}$ ml were designated as a trace.

McAtee (1912) strongly recommended the use of the volumetric method for analyzing food habits. He stated that frequency of occurrence and enumeration gave no indication of the size of food particles and, in most cases, overemphasized foods which were very resistant to digestion. The frequency of occurrence method is the quickest while enumeration is the most time consuming when small food items are present. During this study, all three major methods of analyzing gizzard contents were used to assure maximum accuracy.

Measuring Food Availability.—Because rails feed mostly in shallow water areas, an attempt was made to measure both the flora and fauna of this habitat. A cylindrical bottom sampler with a diameter of 29 inches and height of 20 inches was made of sheet metal and covered an area of $\frac{1}{4000}$ of an acre. The sampler was placed randomly in an area known to be used regularly by rails. The lower edge of the cylinder was forced into the muck to prevent organisms from escaping and water from seeping in; then the muck and water were removed. This sample was then poured through a "tube separator" made out of three sections of stove pipe. Each section contained a screen with a different sized mesh: $\frac{1}{2}$ inch at the top, $\frac{1}{4}$ inch in the middle, and $\frac{1}{16}$ inch at the bottom. These mesh sizes were chosen because they strained out the potential foods but still allowed water and muck to flow through the tube.

FOOD UTILIZATION

Nineteen Soras and thirty-seven Virginia Rails were collected for study. Two Soras and two Virginia Rails were trapped in Jemerson's Slough and one Virginia and three Soras were from Goose Lake. The remaining birds were caught in Smith's Slough. The rails were taken, for the most part, in shallow water of less than 24 inches deep in areas of dense stands of cattail or sedge.

Table 1 shows, for each type of food found, the comparison in per cent, frequency of occurrence, enumeration, and volume. The findings show that seeds occur more often in the food of the Sora than in that of the Virginia Rail, while animal foods occur more often in the food of the Virginia Rail. However, Virginia Rails consumed a much larger amount of duckweed (*Lemna* spp.).

Grit was not included with the foods shown in Table 1 because the differences in the amounts consumed by the two species would bias the volumetric measurements. Therefore, grit was computed as a percentage of the total gizzard contents by the volumetric method. Soras contained an average of 23.2 per cent grit while Virginia Rails contained an average of

TABLE 1
FOOD HABITS OF (19) SORA AND (37) VIRGINIA RAILS
COMPARING THREE DIFFERENT MEASUREMENT INDICES.

Foods consumed	Frequency of occurrence (per cent)		Enumeration (per cent)		Volume (per cent)	
	Sora	Virginia	Sora	Virginia	Sora	Virginia
Adult insects						
Coleoptera	31.5	35.1	0.4	3.7	T	2.4
Calliphoridae	5.2	0	T*	0	0.5	0
Gryllidae	5.2	0	T	0	1.7	0
Hydrophilidae	15.6	40.5	0.2	3.7	0.5	13.7
Curculionidae	5.2	2.7	T	3.7	T	T
Dytiscidae	10.5	37.8	0.2	3.4	T	4.6
Diptera	0	2.7	0	0.2	0	0.2
Odonata	5.2	5.4	T	0.6	8.7	12.1
Notonectidae	0	2.7	0	0.2	0	T
Nitidulidae	5.2	0	T	0	T	0
Unknown	10.5	10.8	—	—	2.4	2.0
Insect larvae						
Hydrophilidae	15.6	32.8	0.2	5.3	T	2.0
Dytiscidae	0	16.2	0	1.5	0	T
Diptera	21.0	43.2	0.3	15.9	T	22.0
Unknown	5.2	10.8	—	—	0.8	1.5
Crayfish						
Decapoda	0	5.4	0	0.3	0	9.1
Unknown animal	15.6	40.5	—	—		9.0
Snail						
<i>Helisoma</i>	10.5	18.9	0.2	3.0	1.2	3.9
<i>Physa</i>	5.2	0	0.7	0.3	T	T
Unknown	42.1	35.1	—	—	1.3	2.1
Vegetation						
<i>Polygonum</i>	52.6	24.3	36.4	3.7	18.0	T
<i>Carex</i>	79.0	35.1	27.8	9.2	21.5	1.7
<i>Setaria</i>	10.5	0	17.2	0	20.0	T
<i>Lemna</i>	31.5	37.8	11.2	44.7	7.9	12.8
<i>Scirpus</i>	5.2	5.4	3.9	T	0.5	T
<i>Agropyron</i>	0	10.8	0	1.1	0	T
Unknown seeds	42.1	8.1	—	—	12.9	0.9

* T = less than .1 per cent.

2.6 per cent grit. The high incidence of grit is characteristic of most seed-eating birds (Berger, 1961).

All three of the techniques of measurements and analysis indicated that there was a definite overlap in the kinds of food eaten by the two species of

TABLE 2
PER CENT ENUMERATION OF POTENTIAL FOODS FOUND IN 21 BOTTOM SAMPLES.

Potential foods	Enumeration (per cent)	Potential foods	Enumeration (per cent)
Vegetation (seeds)		Snails	
<i>Polygonum</i>	24.5	<i>Helisoma</i>	1.1
<i>Carex</i>	11.5	<i>Stagnicola</i>	2.9
<i>Scirpus</i>	3.0	<i>Physa</i>	2.6
<i>Potamogeton</i>	0.3	<i>Gyraulus</i>	1.5
<i>Typha</i>	T*	<i>Planorbula</i>	2.9
Unknown	3.0	<i>Fossoria</i>	T
Insect adults		Leeches	
Diptera	1.1	<i>Erpobdella</i>	2.6
Hydrophilidae	2.2	<i>Helobdella</i>	0.6
Hemiptera	T	Misc. invert.	
Dytiscidae	1.1	<i>Hyaella</i>	20.6
Coleoptera	1.0	<i>Camborus</i>	0.6
Insect larvae		Isoptera	T
Diptera	12.2		
Hydrophilidae	T		
Hemiptera	T		
Coleoptera	1.5		

* T = less than .1 per cent.

rails, but Soras clearly ate a larger amount of plant material than did Virginia Rails. Pospichal and Marshall (1954) found that there was considerable overlap of foods between the two species of rails. Martin, Zim, and Nelson (1951) stated that during the summer the Virginia Rails ate about 3 per cent plant material, while Soras ate 40 per cent plant material. None of these investigators related foods eaten to food available.

FOOD AVAILABILITY IN RELATION TO USE

A total of twenty-one bottom samples was taken with the cylindrical sampler. The locations of the samples were chosen randomly near the trap sites. After a sample was taken and the muck and debris were removed, each potential food item was classified into taxonomic groups and enumerated (Table 2). Weights also were measured, but on a much broader classification than enumeration: for example, seeds, insects, snails, leeches and miscellaneous invertebrates. Table 3 compares percentage composition according to weights and enumeration.

An index rating, based upon Bellrose and Anderson's (1940) method, was used to relate the food-habits of the Sora and Virginia Rails to food availability. Bellrose and Anderson (1940) designated the food habits as

TABLE 3
COMPARISON OF PER CENT WEIGHT AND ENUMERATION OF
POTENTIAL FOODS FOUND IN 21 BOTTOM SAMPLES.

Potential foods	Weight (per cent)	Enumeration (per cent)
Seeds	20.7	42.3
Insects	35.5	20.1
Snails	26.1	11.0
Leeches	13.4	3.2
Misc. Invert.	4.1	21.6

the percentage of foods utilized by the birds, and this was measured by the volumetric method. Food availability or percentage of abundance was based upon acres of various vegetative communities. In the present study, the percentage of foods used by the rails was based on the enumeration of the bottom samples. It was assumed that all foods present were equally available to feeding birds.

Table 4 presents the data on bottom sample contents, per cent used, per cent abundance and utilization index rating of the Sora and Virginia Rails. A rating of 1.0 indicates that the food material was used approximately in proportion to its abundance. A rating of more than 1.0 indicates that the food was preferred by rails and a rating of less than 1.0 would indicate that food was less utilized than its abundance would imply. The index rating showed that the Soras preferred three seed types: *Polygonum*, *Carex*, *Scirpus*, and one insect, hydrophilid larva. The index rating also showed that the Virginia Rails preferred no seeds but selected six insect types: Diptera larva, adult and larval Hydrophilidae, adult Coleoptera, adult dytiscids, Hemiptera adult and one snail, *Helisoma*.

Table 4 indicated that 28.4 per cent of Sora foods and 46.6 per cent of the foods of the Virginia Rail were not found in the bottom samples. However, of these foods, *Lemna* was found 11.2 per cent of the time by enumeration in the Sora and 44.7 per cent in the Virginia Rail. An exact count of each individual duckweed plant was not recorded in the bottom samples, and thus, a utilization index could not be calculated. However, the per cent of surface area covered in each bottom sample by the species was approximated and it was found that all the samples contained from 50 to 100 per cent *Lemna*.

Of the 28.4 per cent of Sora foods not recorded in bottom sample, 17.2 per cent of this was foxtail. Foxtail appeared in only two of the rails. The foxtail group is predominantly a wet-meadow plant, a fact which would account for its not being collected in the bottom samples and also would indicate that the Sora may venture out of the marsh to feed. During the night

TABLE 4
INDEX TO FOOD UTILIZATION BY SORA AND VIRGINIA RAILS, 1963 AND 1964.

Organism found in bottom sample	Per cent used (enumeration)		Per cent abundance (enumeration)	Index rating	
	Sora	Virginia		Sora	Virginia
Seeds					
<i>Polygonum</i>	36.4	3.7	24.5	1.6	0.1
<i>Carex</i>	27.8	9.2	11.5	2.4	0.8
<i>Scirpus</i>	3.9	0.0	3.0	1.3	0.0
<i>Potamogeton</i>	0.0	0.0	0.3	0.0	0.0
<i>Typha</i>	0.0	0.0	0.1	0.0	0.0
<i>Najas</i>	0.0	0.0	0.1	0.0	0.0
Insects					
Diptera larva	0.3	15.9	12.2	0.2	1.3
Diptera adult	0.0	0.2	1.1	0.0	0.2
Hydrophilidae adult	0.2	3.7	2.2	0.1	1.7
Hydrophilidae larva	0.2	5.3	0.2	1.0	2.6
Hemiptera adult	0.0	0.2	0.2	0.0	1.0
Hemiptera larva	0.0	0.0	1.3	0.0	0.0
Coleoptera adult	0.4	3.7	2.0	0.2	1.8
Dytiscidae adult	0.2	3.5	1.1	0.2	1.7
Snails					
<i>Helisoma</i>	0.2	3.0	1.1	0.2	2.7
<i>Stagnicola</i>	0.0	0.0	2.9	0.0	0.0
<i>Physa</i>	0.6	0.3	2.6	0.2	0.1
<i>Gyraulis</i>	0.0	0.0	1.5	0.0	0.0
<i>Planorbula</i>	0.0	0.0	2.9	0.0	0.0
Leeches					
<i>Erpobdella</i>	0.0	0.0	2.7	0.0	0.0
<i>Helobdella</i>	0.0	0.0	0.6	0.0	0.0
Misc. Invert.					
<i>Hyalolla</i>	0.0	0.0	20.6	0.0	0.0
<i>Camborus</i>	0.0	0.0	0.6	0.0	0.0
Isoptera	0.0	0.0	0.1	0.0	0.0
Foods not found in bottom sample					
<i>Agropyron</i>	0.0	1.1			
<i>Setaria</i>	17.2	0.0			
Notonectidae	0.0	0.2			
Odonata	0.0	0.6			
<i>Lemna</i>	11.2	44.7			

of 15 August 1963, a Sora was seen in a cultivated field approximately three miles from any marsh habitat.

In the Virginia Rails, 1.1 per cent of the total food not recorded in the bottom sample was quackgrass, another wet-meadow plant, which also indi-

cates that Virginia Rails may feed in the uplands. The remaining 4.8 per cent of the Virginia Rails food not recorded in the bottom sample consisted of insects.

DISCUSSION

Gause's (1943) principle states that two species with identical ecological requirements cannot live in the same niche. If two species of birds live in the same habitat in the same region, eat the same types of food, and have the same ecological requirements, there will be direct competition between the two species, and one may be eliminated. Grinnell (1904) said that two species can live together only by adaptation to different sorts of foods or modes of food getting. Lack (1944), in his survey of the ecology of passerine birds of Galapagos Islands, showed that similar species occurring together in the same habitat tended to differ from each other in feeding habits and associated morphology of the beak.

The two species of rails observed in this study had some similarities but also major differences in their diets. The Sora, having a heavy short beak, eats approximately 73 per cent seeds, volumetrically. The Virginia Rail, with its long slender decurved beak, eats nearly 62 per cent insects, volumetrically. These differences in food habits between the two species of rails suggest that the two species can live together successfully without serious competition for food.

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8 AUGUST 1968.

A NEW TURKEY FROM THE PLIOCENE OF NEBRASKA

LARRY D. MARTIN AND JAMES TATE, JR.

A study of avian fossil material from the Upper Pliocene of Nebraska has revealed the presence of a new genus and species of turkey (Meleagrididae). The type specimen and the referred material are deposited in the University of Nebraska State Museum Collections (UNSM).

This material, including two left coracoids (UNSM 20033, complete and 20034, humeral $\frac{1}{3}$), two ♀ tarsometatarsi (UNSM 20037, lacking trochlea and 20035, proximal $\frac{2}{3}$), and a spur core (UNSM 20036), was collected from the lower part of the Kimball Formation, UNSM Coll. Loc. Ft-40, south of Lime Creek in Frontier County, Nebraska. The Kimball Formation is the upper formation of the Ogallala Group and is older than the San Pedro Formation of Arizona and the Rexroad Formation of Kansas, in which *Agriocharis progenes* Brodkorb occurs. A discussion of the stratigraphy of the Ogallala Group is outlined by Schultz and Stout (1961:7,9, Fig. 3). Vertebrate faunal lists for the Kimball Formation have been published by Schultz and Stout (1948:557, Table 1), modified by Kent (1963:14, Table 1) and include: *Megalonyx*; *Hypolagus*; *Perognathus*; *Thomomys*; *Dipoides stirtoni* Wilson; *Dipoides williamsi* Stirton; saber-toothed tiger (undet.); *Amebelodon fricki* Barbour; *Teleoceras*; *Neohipparion*; *Pliohippus* (*Astrohippus*); *Pliohippus* (*Dinohippus*); *Nannipus*; *Prosthenops*; *Procamelus*; *Pliauchenia*; *Cranioceras*; *Texoceros guymonensis* Frick; *Sphenophalos middleswarti* Barbour and Schultz; *Citellus kimballensis* Kent; and *Aphelops kimballensis* Tanner.

Proagriocharis gen. nov.

Type species.—*Proagriocharis kimballensis* Martin and Tate

Diagnosis.—Agrees with the Meleagrididae in having the median surface of the head on the coracoid flattened (also flattened in the Cracidae, but it is notched in the Tetraonidae and Phasianidae); brachial tuberosity lacking overhang (present in Tetraonidae and Phasianidae), and the scapular facet concave. Tarsometatarsus long and slender as in female turkeys and some Phasianidae (relatively short and stout in the Cracidae and Tetraonidae); inner calcaneal ridge long as in most Meleagrididae, most Tetraonidae, and most Phasianidae (ridge short in Cracidae, *Gallus* and other Galliformes).

Proagriocharis differs from other genera of turkeys in having the following combination of characters: Coracoid resembling *Parapavo* and differing from *Meleagris* and *Agriocharis* in that the scapular facet is nearly rounded rather than elongate; the procoracoid is blunted, and the shape of the head is oval with indistinct mid-ventral notch. It resembles *Agriocharis* and differs

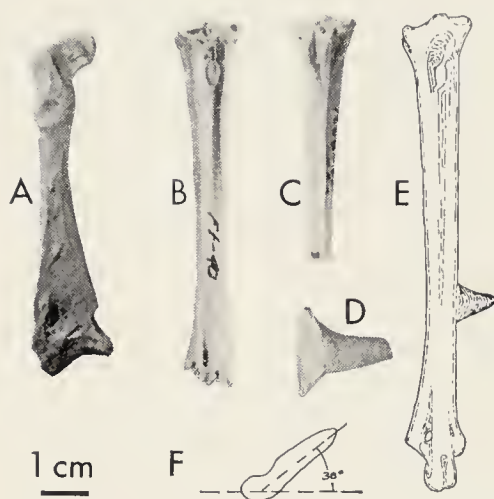


FIG. 1. A. Holotype of *Proagriocharis kimballensis* (UNSM 20033), left coracoid. B. Referred right tarsometatarsus (UNSM 20037), anterior view. C. Referred left partial tarsometatarsus (UNSM 20035), posterior view. D. Referred left spur core (UNSM 20036). E. Drawing of cast of right male tarsometatarsus, anterior view (see text). F. Cross section of right tarsometatarsus and spur core showing angle at which spur stands with the frontal plane of the bone.

from *Parapavo* and *Meleagris* in that the head is raised above the inner surface of the neck. *Proagriocharis* differs from the other genera of turkeys in the shape of the coraco-humeral ligamental attachment which is elongate and lacks a distinct border on the outer side of the neck (triangular and having a distinct border on the outer side of the bone in the other Meleagrididae (Howard, 1927:6)). It also differs from the other three genera in that the pneumatic fossa is smaller and the triosseal canal is deeper so that the inner surface of the neck just below the head is reduced, producing a much thinner neck. The head is free from the neck for a greater distance than in any other turkey.

The tarsometatarsus resembles *Agriocharis* and differs from *Parapavo* and *Meleagris* in the angle of the spur core to the acrotarsal surface (less than 60° ; greater for *Parapavo* and *Meleagris*, less for *Agriocharis*). The spur core (cast) is more proximally placed (42 per cent of the total length) than it is in *Agriocharis ocellata* (36 per cent of the total length), and just overlaps the lower range of *Parapavo* and *Meleagris* in this respect.

***Proagriocharis kimballensis* sp. nov.**

Holotype.—Left coracoid (Fig. 1A), UNSM 20033 from UNSM Coll. Loc. Ft-40, south of Lime Creek, E $\frac{1}{2}$, E $\frac{1}{2}$, SW $\frac{1}{4}$, Sec. 15, T5N, R26W, Frontier County, Nebraska. The stratigraphic occurrence is Pliocene, Ogallala Group, Kimball Formation.

TABLE 1
MEASUREMENTS IN MILLIMETERS OF TWO BONES FROM *PROACRIOCHARIS*
KIMBALLENSIS MARTIN AND TATE, AND *ACRIOCHARIS* *PROGENES* BRODKORB.

Measurement	<i>P. kimballensis</i>	<i>A. progenes</i> (Brodkorb, 1964)
Coracoid	UNSM 20033	
Total length	66	—
Length to pneumatic foramen	58	65
Head through scapular facet	23	31
Width of head	9	10.8
Least width of shaft	6	10.1
Tarsometatarsus	UNSM 20037 ♀	
Width proximal end	13	—
Length to top distal foramen	69	—

Referred material.—The humeral end of a left coracoid, UNSM 20034. A right tarsometatarsus lacking the trochlea, UNSM 20037 (Fig. 1B). The proximal end and greater part of the shaft of the left tarsometatarsus UNSM 20035 (Fig. 1C) and an isolated left spur core UNSM 20036 (Fig. 1D). All of this material is from the same locality and horizon as the holotype.

In the collections of the University of Nebraska State Museum there is also a cast (UNSM 20038) of an almost complete right male tarsometatarsus here referred to *Proagriocharis kimballensis*, from the type locality (Fig. 1E). The original was in the private collection of Alex Keith (now deceased), who owned the property on which UNSM Coll. Loc. Ft-40 is situated. The whereabouts of the original specimen is presently unknown.

Diagnosis.—Coracoid very small; flexure of the humeral end 63° to the axis of the shaft. Outer posterior intermuscular line curving away from the outer border of the shaft more than in *Parapavo*, *Meleagris*, or *Agriocharis ocellata* cutting across the dorsal surface of the shaft just above the midpoint. The inner posterior intermuscular line curving in from the inner border of the shaft more than in the other turkeys. The intermuscular lines similar in general form to those found in some of the Tetraonidae (i.e., *Tympanuchus cupido*). The sterno-coracoidal process less developed than in *Parapavo*, *Meleagris*, or *Agriocharis ocellata* extending only slightly beyond the sternal facet.

Tarsometatarsus represented by two mature female specimens, and a spur core. The spur core long and well shaped as in *Agriocharis*. Tarsometatarsus thin, tapering distally. An incipient third ridge between the inner and outer ridges of the hypotarsus; the facet for the first toe (hallux) high and pos-

teriorly situated; the inner distal foramen a small depression. The cast shows a small, penetrating inner distal foramen.

The following measurements are taken from the cast and therefore probably differ slightly from the original: total length 98 mm, length to top of the distal foramen 84 mm, width of the proximal end 14 mm, height of middle of spur core 40 mm above tip of middle trochlea, angle of spur core to the acrotarsial surface 38° (Fig. 1F).

DISCUSSION

Proagriocharis kimballensis appears to be the oldest and smallest species of turkey described to date. *Agriocharis crassipes* from the Late Pleistocene of Mexico also has a small coracoid, but it is stouter and the tarsometatarsus of *A. crassipes* is larger as well as being more heavily built. The spur core is set at about the same angle (39°) as it is in *Proagriocharis kimballensis* and is only slightly more proximal in position (45 per cent of the length of the shaft). In these features *Agriocharis crassipes* is closer to the new genus than it is to any of the other described species of *Agriocharis*. *Proagriocharis* was a turkey about the size of a Sage Grouse (*Centrocercus urophasianus*) with slim feet and a slender spur core. Miller (1940:156), described *Agriocharis crassipes* as “. . . a bird with small body and wings, but with tremendously heavy feet, armed with an unusually stout spur.”

Agriocharis leopoldi (Miller and Bowman) and *A. progenes* Brodkorb are the two turkeys closest in time to *Proagriocharis* as both are Blancan in age (regarded as Early Pleistocene in this paper (see Flint, 1965)). *Proagriocharis* may be a suitable ancestor for both species, but they are not presently included in the new genus because of the difference in the placement of the spur core in these species. *Agriocharis leopoldi* has the spur core at a much greater angle ($53\text{--}58.5^\circ$) and placed slightly lower (39.8 per cent of the total length) than it is in *Proagriocharis* (see Miller and Bowman, 1956:44). *Agriocharis progenes* has the angle of the spur core slightly less (50°) and the core slightly more distally placed than in *A. leopoldi*. *A. progenes* lacks the pneumatic fossa on the dorsal base of the shaft of the scapula (Brodkorb, 1964:226), and this might be expected to be absent from the scapula of *Proagriocharis* also. Both *Agriocharis leopoldi* and *A. progenes* are much larger than *Proagriocharis kimballensis*.

Although the coracoid has several features in common with *Parapavo*, *Proagriocharis* seems to have its greatest overall resemblance to *Agriocharis*. Despite their separation in time there is a great similarity in size between *A. crassipes* and *Proagriocharis*. This is probably due to a secondary development of small body size in *Agriocharis crassipes* by the late Pleistocene. *A. crassipes* differs from *Proagriocharis* in the proportions of the limb bones

which are much heavier in the former. The evolution of the turkeys during the Pleistocene was apparently explosive. Three genera and eight species (*Agriocharis leopoldi*, *A. progenes*, *A. anza*, *A. crassipes*, *A. ocellata*, *Meleagris alta*, *Meleagris gallopavo*, and *Parapavo californicus*) are probably all sound species, most of which appear to have developed during the Pleistocene. Modern turkeys represent a depauperate group by contrast, with only two surviving species.

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GENERAL NOTES

Conjoined twin Darwin's Rhea.—On 20 March 1969, a Darwin's Rhea (*Pterocnemia pennata*) egg was opened at the New York Zoological Park and was found to contain conjoined twin embryos. The egg was laid on 30 January 1969 and six days later, was placed in a forced-air incubator. By 17 March, movement was heard within the shell. Movement continued until noon on 19 March, when no signs of life could be detected. Other Darwin's Rhea eggs incubated under the same conditions (97° F and 85 per cent relative humidity) had an average incubation period of 37 to 39 days. After 43 days of incubation, this egg was opened and the conjoined twins discovered.



FIG. 1. Embryo of conjoined twin Darwin's Rhea.

The embryos are joined and single ventrally from the lower mandible, to the sternum, and yolk sac. Dorsally the embryos are double with two sets of vertebrae, two sets of limbs, and basically, two separate bodies. Two separate upper mandibles fused at their base into one head with only one pair of eyes. At the back of the skull, two sets of vertebrae meet. The cranium was incomplete and 2.5 cm² of the brain was exposed. (see Fig. 1.)

The twin embryo weighed 364 g while the yolk and yolk sac weighed approximately 100 g for a total of 464 g. Thirty-five normal newly hatched chicks averaged 426 g but varied from a low of 327 g to a high of 491 g. The eggshell itself weighed 84 g and varied from 0.040 to 0.042 inch in thickness. All of the waste material and the membranes from around the embryos totaled 65 g. The egg had lost 55 g or 8.2 per cent of its weight during development. An 8.2 per cent weight loss is 0.8 per cent above the average weight loss found in 30 Darwin's Rhea eggs, at the New York Zoological Park, but is well below the maximum of 8.8 per cent that occurred in one other Darwin's Rhea egg which hatched successfully.

The specimen is preserved in a buffered formalin solution. I thank W. G. Conway for comments upon the manuscript.—DONALD BRUNING, *New York Zoological Society, Bronx Park, Bronx, New York 10460, 8 May 1969.*

A swimming Bald Eagle.—During my 14-year residence in Alaska I have many times observed Bald Eagles (*Haliaeetus leucocephalus*) plucking floating food from the surface of the water, and have heard reports of them entering the water in pursuit of live fish or ducks. Such incidents may be common, but there are few descriptions in the literature. Bent (Life histories of North American birds of prey, Part I. Dover Publications, Inc., New York, 1961.) referred to several instances, but none of them involved an eagle actually swimming. On the morning of 10 March 1969, at the oceanside laboratory of the U. S. Bureau of Commercial Fisheries at Auke Bay, Alaska, I witnessed an incident which demonstrated that an eagle can land on the water and regain its normal aerial environment after "swimming" to shore with captured prey.

The incident involved a mature Bald Eagle and its prey, probably a female Barrow's Goldeneye (*Bucephala islandica*). The duck was one of about a dozen in calm water about 25 yards from shore. The eagle was perched in the top of a tall spruce tree at the water's edge, from which it launched itself on a steep glide toward the ducks. The ducks recognized their danger and attempted to escape by flying or diving. The eagle plunged into the water, intercepting one of the ducks that had already dived below the water surface. The eagle then calmly folded its wings and floated on the surface for about 2 minutes before attempting to reach shore. The duck was presumably being drowned during this wait and probably provided some buoyancy to the eagle.

Finally, the floating eagle propelled itself toward shore by slow rhythmic beats of its outstretched wings, much like a human swimmer using the butterfly breast stroke. It rode high in the water, so that on the forward motion of each stroke, both wings were simultaneously lifted almost clear of the water surface. The eagle reached shore, with the dead duck clutched in its talons. After resting for about 30 seconds, the eagle flew across the water carrying the duck, without having relaxed or changed its grip.—THEODORE R. MERRELL, JR., *Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821, 26 May 1969.*

Sharp-tailed Grouse gives aggressive display to automobiles.—Recently, while driving with my family on a busy four-lane divided highway I noticed a Sharp-tailed Grouse (*Pedioecetes phasianellus*) on the grassed dividing strip run briefly towards us with its head lowered and neck outstretched in an aggressive manner. All this happened in a matter of seconds, but it left a vivid impression because it seemed so improbable. Accordingly, as soon as we found a place to turn around, we drove back along the opposite side of the highway until we could see the grouse. We then drove slowly along on the shoulder of the road and parked about 50 feet from the grouse, which seemed to pay no attention to us. It was, however, still busily chasing passing cars. This was at 16:30 on 27 April 1969, on the Perimeter Highway close to Highway No. 59, southeast of Winnipeg, Manitoba. It was a bright day and we had an excellent view of the bird for the sun was behind us.

The grouse was making a pass at each approaching car, first turning to face it, then, when the car reached a certain distance, running towards it and suddenly veering as the car passed. Sometimes it ran briefly alongside the car before turning back, but in any case it usually ran in a curved path. It seemed to be threatening each approaching car then driving it off, so to speak, and the results presumably satisfied it for as each challenged car pulled away the grouse ceased to pursue it and either turned to the next car or stood still. Inasmuch as vehicles, both cars and trucks, were moving by in good numbers the grouse was kept fairly busy. In one five-minute period it made passes at 15 assorted vehicles that drove by at various speeds on both sides of the center strip. These dashes towards approaching cars varied in length from a few feet to about 20 feet and depended upon the position of the bird in respect to the car when the bird first began to make its run. When a car approached after a lapse in traffic the grouse was in a position to make a run of some length, but when cars were passing in rapid succession it sometimes lunged at first one car and then another with hardly a pause. All this while it kept within an interval of about 40 or 50 feet, shifting back and forth as traffic varied in either direction. It thus occupied a territory about 50 feet in length and 20 feet wide, the latter being the width of the grassed divider. It also, and this seemed reasonable, kept back about six inches from the edge of the curb on both sides.

During the 45 minutes that we watched this performance the grouse stopped chasing vehicles only twice. Its behavior then suggested that it had tired and was resting and indeed on one occasion it was lying down. Its rest periods were brief and in each case passing cars seemed to stimulate it to resume its peculiar game. On three or four occasions during traffic lulls it stood with wings held out sideways, head lowered, tail cocked, and then gave a few soft hoots—part of the typical display of a Sharp-tailed Grouse on its dancing ground. It also gave a few “chuckling” notes during these displays. I watched it closely with binoculars at these times and did not notice that it inflated its air sacs, but the display was clearly at a relatively low level. The eye-comb was pale yellow and appeared to be limited to a short strip anterior to the eye, rather than extending over the eye as expected. Presumably this was a subadult bird or one just coming into breeding condition.

Several times it paused briefly to feed. Later, upon inspecting the site I found a sparse strip of oats growing in the grass down the center of the area. The strip had been mowed at some time during the previous year and oat heads were scattered about on the ground. It seems reasonable to suppose that the grouse had been attracted by this source of food and had then responded aggressively to passing cars.

Evidence that the oats continued to prove attractive to grouse in the vicinity was obtained on 28 June when a female Sharp-tailed Grouse with oat kernels in its crop was found dead on the highway and close to the center strip in the same place that the male had occupied.

The reactions of Ruffed Grouse (*Bonasa umbellus*) to automobiles with running motors has attracted some attention (Bump et al, *The Ruffed Grouse*. New York State Cons. Dept., 1947, pp. 262-264) the sound of the motor being assumed to have some relation to the sound of grouse drumming, but I know of no similar reports for Sharp-tailed Grouse.

Our period of observation ended abruptly at 17:15 when a car stopped about 300 yards away on an adjacent roadway about 50 yards south of the highway and a man got out to walk a dog. The grouse at once flew off strongly to the southwest for almost a mile before we lost sight of it. On the following day and on several days thereafter a number of observers visited the area, but the grouse was not seen again on the center strip. At least three grouse were seen, however, on the access road to the south. When first sighted in the morning of 28 April these were displaying as if on a dancing ground. It is presumed that the bird that had chased the automobiles was one of these or at least a member of a group that was meeting close to the highway.—ROBERT W. NERO, *Manitoba Museum of Man and Nature, 190 Rupert Avenue, Winnipeg, Manitoba, 16 June 1969.*

Ring-billed Gull and Laughing Gull catch fish by “ploughing” and “skimming.”—On 27 April 1969 I was watching two Ring-billed Gulls (*Larus delawarensis*) catching fish (probably *Fundulus* sp.) along the edge of rising tide waters in a small estuary (Gulf Pond) in Milford, Connecticut. Both birds were feeding by the method called “ploughing” by Zusi (Wilson Bull., 80:491-492, 1968) in his report of observations of Greater Yellowlegs (*Totanus melanoleucus*). In ploughing the bird runs through shallow water with the lower mandible cutting the surface of the water, seizing any prey contacted. On 9 September and 21 September 1969 in the same locality I saw ploughing by small (6-9) groups of Laughing Gulls (*Larus atricilla*), accompanied on the 21st by similar numbers of Ring-bills. Again these birds were catching small fish near the water's edge. On several occasions a bout of ploughing appeared to have been stimulated by a Greater Yellowlegs ploughing the margin, with gulls then flying in from mudflats 20-40 meters away.

One of the Ring-bills on 27 April was also seen capturing a fish by “skimming.” This individual had been flying back and forth along the water's edge at a height of about 10 feet. It turned and dived suddenly, almost to the surface of the water. For a period of 2-4 seconds it skimmed over the surface, with the lower mandible cutting the water (exactly like a Black Skimmer (*Rhynchops nigra*). While still in flight, the gull caught a small fish; it landed immediately and swallowed the fish. I saw this gull apparently skimming several times, but only once could I be sure that the prey was captured while the bird was in flight. On 9 and 21 September an approach to skimming was seen in Laughing Gulls, resembling the skimming described above, except that the birds made hopping or paddling motions with their feet touching the water; during each flight the lower mandible remained constantly immersed.

On a number of occasions I have seen Ring-bills ploughing, but I know of no previous observation of feeding by skimming in either species.

I am grateful to Dr. N. Philip Ashmole for advice on preparation of this note.—KARL ERIC TOLONEN, *Peabody Museum of Natural History, Division of Vertebrate Zoology, Yale University, New Haven, Connecticut 06520, 25 September 1969.*

A putative skeletal specimen of the Flammulated Owl with Alabama locality data.—Several years ago Gid E. Nelson, Jr., gave me over 100 bird skeletons, among which was the complete skeleton and rhamphotheca of a fully grown, small owl. The specimen bears the locality of Shelby County, Alabama. The original label lists Montevallo, where Nelson then resided, however, no town is indicated in his catalog. The date listed is November 1953. The sex was not determined.

Although previously identified as *Otus asio*, study of its remains indicates the specimen is from a smaller species of *Otus*, which on geographic grounds must be the Flammulated Owl (*O. flammeolus*). The smooth texture of the surface of the bones indicates the bird is fully grown and thus its size can be compared with other adult specimens. Ten species of *Otus* occur in the Western Hemisphere north of South America (Eisenmann, 1955; Peters, 1940). Measurements of the culmen for the 9 species excluding *O. flammeolus* range from 10.5 to 17.5 mm (Ridgway, 1914; Wetmore, 1968). The range for the latter species is 8.5 to 10 mm. The rhamphotheca of the Alabama *Otus* is free from the underlying bone and worn slightly from the maceration cleaning process, but its culmen certainly measured less than 10 mm.

The diminutive Flammulated Owl is known to have especially small feet (Miller, 1933). To support further the identity of the specimen as *O. flammeolus* I compared its tarsometatarsal length of 22.6 mm with that of 5 species of *Otus*, including the only 3 recorded from the United States (A.O.U., 1957). A total of 100 *Otus asio* ranged from 28.3 to 37.7 mm with a mean of 32.85. This sample consists of 9 North American races including the small western *O. a. gilmani*. *O. a. floridanus* is represented by 30 individuals, 19 of which are smaller than all specimens of other races. The tarsometatarsus ranged from 28.3 to 32.8 mm with a mean of 30.69 in these *O. a. floridanus*. For the remaining 70 specimens the range is 31.1 to 37.7 with a mean of 33.77. No sexual dimorphism in tarsometatarsal length was evident. Two *O. trichopsis* measure 31.0 and 32.0 mm. Four *O. flammeolus* range from 21.9 to 24.3 (mean 23.00) which nicely encompasses the measurement of the unknown. One specimen of the Old World *O. spilocephalus* measures 28.9 mm, too large to include the unknown. However, one *O. scops*, which some workers consider conspecific with *O. flammeolus* (Eisenmann, 1955), measures 23.7 mm. Assuming the owl is a species known to inhabit North or Central America, measurements indicate it is *O. flammeolus*.

Circumstantial evidence supports the contention that the specimen, indeed, did come from Shelby County, Alabama. All but one of the 100 specimens given me were collected in the same county, Nelson never collected within the known range of *O. flammeolus* nor did he have any students that did, and no discrepancies between any of his specimens and their appended data have been noted. Alabama College, where Nelson then was employed, is a small school and most of the students came from nearby. He can think of no persons locally who kept live birds. Nelson did not shoot the owl and suspects it was found dead, although he cannot recall the specific incident (all pers. comm.).

These factors do not eliminate the possibility that the specimen came from elsewhere and was transported, intentionally or accidentally, to Alabama. Similar criticism can be levied against most specimens and the problem is going to become increasingly acute as man increases in number and mobility. I suggest as a general policy that if an investigator can find no evidence to the contrary such distribution records be published along with the circumstances and leave the decision of the validity of the record to the reader.

For those willing to accept this record, it constitutes the first Flammulated Owl from Alabama, and only the second from eastern United States. Normally the species is found in western North America from British Columbia to Guatemala, however, one was taken live at Baton Rouge, Louisiana, on 2 January 1949 (Lowery, 1955). Again if accepted, this record has implications regarding the migratory status of the species which at present is controversial (Johnson, 1963). It is common for migratory birds that breed in western North America to appear in southeastern United States in fall and winter, and an above average flux occurred in 1953 (Audubon Field Notes, 1954). It seems far less likely that a sedentary land bird would stray almost 1,000 miles from its normal range.

An additional value of this record is to make people aware of the possibility of overlooking specimens of the Flammulated Owl. Nelson is an ornithologist by training yet he handled this specimen without ever realizing it was something other than the locally common *Otus asio*.

I am grateful to Sievert A. Rohwer who measured the large series of *Otus asio* in the University of Kansas Museum of Natural History, Ned K. Johnson who loaned certain specimens from the University of California Museum of Vertebrate Zoology, and Norman L. Ford who corroborated my identification. The remaining measurements were taken from specimens in the Pierce Brodkorb collection at the University of Florida, the United States National Museum, and my own collection.

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GLEN E. WOOLFENDEN, *Department of Zoology, University of South Florida, Tampa, Florida 33620, 11 April 1969.*

The double-scratch in the Seaside Sparrow.—Harrison's (Wilson Bull., 79:22-27, 1967) list of genera of the subfamily Emberizinae for which the double-scratch had been recorded did not include *Ammospiza*.

On 8 December 1968 I observed a captive Seaside Sparrow (*Ammospiza maritima*) engage in the double-scratch several times in a period of a few minutes. This backward-kicking movement of both feet was performed while the bird was in an indoor 10 × 12 foot room, the floor of which was covered with dirt and had *Spartina alterniflora* stalks stuck into and held erect by the dirt. The bird double-scratched in a small open area of loose dry dirt with a few millet seeds scattered about.

Whenever I have observed this species feeding in the wild, it generally fed in mud, walking about in a deliberate fashion. But an occasion for the use of the double-scratch might be provided by the occurrence at times in tidal marshes of extensive drifts of *Spartina* seed (which is eaten by this generally insectivorous bird). The fact that feeding Seaside Sparrows are difficult to observe in the thick vegetation of a salt marsh may help explain the lack of previous reports of this double-scratch behaviorism from this species—FRANK ENDERS, *Department of Zoology, Duke University, Durham, N.C. 27706, 1 April 1969.*

Nest-building, incubation period, and fledging in the Black-chinned Hummingbird.—On 14 April 1964 a female Black-chinned Hummingbird (*Archilochus alexandri*) appeared in the English ivy (*Hedera helix*) outside our family room in Phoenix, Arizona, apparently looking for a nesting site. It continued to look on 15 April, selected a spot on 16 April and worked on the nest throughout the day. On 17 April it started working at 07:00 and continued building during most of the day. It was still working on the nest on 18 April but not as consistently as on the preceding days. The nest appeared to be finished in 19 April. The nest was two meters above the ground and 0.25 meters from the picture window. It was constructed of oleander seeds (*Nerium oleander*), spider webs, feathers, and mulberry blossoms (*Morus* sp.). The female spent about 15 seconds at the nest arranging material and was gone about a minute and a half before returning with additional material. This was the pattern on 17 April.

Both eggs were laid on 20 April, one early in the morning and the other late in the afternoon. The female began incubating on 21 April. The male was not seen.

On 3 May the female added bits of white paint from our house to the outside of the nest.

One egg hatched on 7 May after an incubation period of 16 days. The other egg did not hatch. The female began feeding the nestling on 8 May.

The young bird moved out of the nest at 15:00 on 28 May, returned at 16:30, and left the nest at 18:20. It remained in the ivy vines for two days, while the female continued to feed it.

I wish to thank E. M. Reilly, Jr., and Stephen M. Russell for reading and criticizing this note, and Eleanor Radke for putting my notes into correct form.—SALOME ROSS DEMAREE, *148 West Rose Lane, Phoenix, Arizona 85013, 16 June 1969.*

Activity of migrant thrushes as determined by radio-telemetry.—During the spring and fall *Hylocichla* thrush migrations from 1965 through 1968, 88 thrushes were tagged with radio-transmitters as described in Graber (*Audubon Mag.*, 67:368-374, 1965), and in Cochran et al. (*Living Bird*, 6:213-225, 1967).

Due to signal propagation characteristics, even slight movements of radio-tagged birds (such as shifting position on a perch) resulted in audible signal variations. Approximately 500 hours were spent noting these signal variations during periods from sunset to sunrise. During the fall of 1968 an additional 350 hours of thrush activity were recorded by connecting the receiver output to a strip-chart recorder.

Data were obtained for Hermit Thrush (*Hylocichla guttata*), Swainson's Thrush (*H. ustulata*), Gray-cheeked Thrush (*H. minima*), and Veery (*H. fuscescens*). The frequency and temporal pattern of movements were similar for all the above species.

Typically, diurnal activity began about 20 minutes before sunrise, ceased about 20 minutes before sunset, and consisted of intermittent movement interspersed with 5 to 15 minute periods of no movement (Fig. 1).

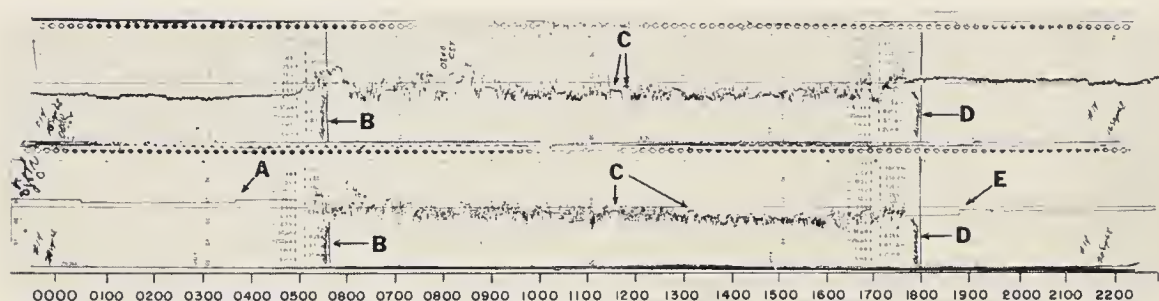


FIG. 1. Strip-chart activity record of an adult Gray-cheeked Thrush on 16 September and 20 September 1968. Times shown are Central Standard. The fuzziness and irregularity of the record before sunrise and after sunset of 16 September was due to fluctuating power line noise. A: A single nocturnal perch movement. B: Sunrise. C: Diurnal periods of no movement. D: Sunset. E: A nocturnal flight lasting about 20 seconds.

Typical nocturnal activity consisted of little or no movement. On 30 per cent of the approximately 220 bird-nights, no movement whatsoever was noted (one radio-tagged bird observed for one night is one bird-night). One to four movements lasting less than a few seconds each were noted on 65 per cent of the bird-nights. Flights lasting less than one minute were observed on 11 occasions (about 5 per cent of the bird-nights).

During the study the initiation of 25 migratory flights was observed. Thrushes began migratory flights after evenings of no movement, a few movements, and after short flights. However, six of 11 short flights were not followed by migratory flights. So far, no *zugunruhe* nor any other activity pattern, diurnal or nocturnal, has been found to regularly precede migratory flight. There was nothing in the bird's behavior, even in the last seconds before take-off, to indicate that a migratory flight was about to take place.

This research was supported by National Science Foundation Grants GB 3155 and GB 6680.—CHARLES G. KJOS AND WILLIAM W. COCHRAN, *Illinois State Natural History Survey, Urbana, Illinois, 20 June 1969.*

First specimens of Chestnut-collared Longspur and Little Gull from Connecticut.—A Chestnut-collared Longspur (*Calcarius ornatus*) was collected on 29 August 1968 at Lordship Beach, Stratford, Fairfield County, Connecticut. The bird was associated with a resident family of Horned Larks (*Eremophila alpestris*). Although the gonads were destroyed, the specimen was identified as an adult female by comparison of plumage with a large series of longspurs at the American Museum of Natural History.

This specimen represents the first Chestnut-collared Longspur taken in Connecticut and the ninth from northeastern North America. All of these were collected close to salt water and the majority (7 of 9) were obtained in the period from 2 June through 14 September. A possible corresponding phenomenon with eastern land birds appearing accidentally on the west coast during the summer has been illustrated by Tenaza (Condor, 69:579-585, 1967) in California.

At the same locality in Stratford, a Little Gull (*Larus minutus*) was collected on 20 June 1969. The bird was an immature female in heavy molt. Immature Little Gulls were observed in coastal Massachusetts during the summers of 1944 and 1953 (Griscom and Snyder, *The birds of Massachusetts*, 1955). The collected bird represents the first specimen of *Larus minutus* from Connecticut and now, along with the longspur, is in the University of Connecticut Museum.—WALTER BULMER, *Environmental and Systematic Biology, Life Science Building, U. of Connecticut, Storrs, Connecticut, 20 July 1969.*

Circle-soaring by migrating nighthawks.—Common Nighthawks (*Chordeiles minor*) rarely soar in circles in an updraft in the manner of Broad-winged Hawks (*Buteo platypterus*). Ellarson (*Passenger Pigeon* 30:115, 1968) presents an account of a flock of approximately 15 migrating nighthawks soaring in circles and notes that there appears to be no other published account of the phenomenon. I have no recollection of observing circle-soaring by nighthawks in some 15 years of watching fall migration at the Cedar Grove Ornithological Station on the western shore of Lake Michigan. I did observe tens of thousands of migrating nighthawks at this locality with as many as 18,000 seen in one day (31 August 1958).

I have observed circle-soaring by nighthawks on three occasions: (1) About 10 individuals near Fitchburg, Wisconsin, in late August or early September, (2) about 15 individuals in Lexington, Ohio, on 8 September 1966, and (3) A concentration of at least several thousand individuals in Columbus, Ohio, on 3 September 1968. The massed movement of nighthawks was first noted at approximately the time of sunset. Hundreds of individuals were seen moving southwest at an altitude of less than 100 feet over the campus of Ohio State University. Other individuals were noted at greater heights, apparently moving randomly. A large, circling flock of perhaps 300 birds was then noted to the east, over the city of Columbus. The massed, low altitude movement largely ceased, and although nighthawks were to be found at low and other altitudes it was difficult to discern any predominant direction of movement. The birds formed into large circling flocks on several occasions during the observation period of approximately one half-hour. There was at least one flock of circle-soaring nighthawks in the air during all of this time. The minimum number of circle-soaring birds exceeded 200 at any time during the half-hour. At one time there were three flocks in view, one containing between 500 and 800 birds. At least one flock rose to the limits of unassisted vision and its pattern of dissolution or movement could not be determined in the failing light. Although a number of nighthawks were observed perched as darkness fell, there were relatively few nighthawks in the area the next morning. This suggests that many of the high-soaring birds left the area at dusk or during the night.

Further observation during late August and early September at suitable observation points away from leading lines may reveal this to be a not uncommon mode of migration for the nighthawk.—HELMUT C. MUELLER, *The University of North Carolina, Chapel Hill, North Carolina 27514, 11 April 1969.*

Method of searching for food by the Swainson's Warbler.—The Swainson's Warbler (*Limnothlypis swainsonii*) is primarily a ground feeder, foraging in a manner generally different from that of other ground-feeding parulids. In searching for food, usually in dry leaf litter, its gait is described by Brewster (*Auk*, 2:65–80, 1885) as “distinctly a walk.” Norris (*Contrib. Charleston (S.C.) Mus.*, 9:78, 1963) also observed that it walked, and that its “gait was rather rapid and jerky, suggestive of that of the starling.” He further stated that the Swainson's Warbler may hop “when traversing leaf litter.” During 40 hours of observation of the ground locomotion of this species, I would prefer to describe it as hopping some of the time, though mostly it moves in a rather rapid step that is sort of a cross between a walk and a hop, suggesting a canter.

Insects, the Swainson's principal food, are located as the bird pokes its bill under a leaf, pushing it upwards, searching the ground beneath it, or examining its underside. A leaf may be held up momentarily and tilted at an angle as the bird inspects the underside; and if a leaf is curled, it is opened as the bird inserts and spreads apart its mandibles. Sometimes, as the bird moves rapidly forward, lifting or shoving leaves upward, most of its body disappears beneath a pile of leaves.

The Swainson's Warbler occasionally obtains food from the surface of the leaf litter or the top of a log, or by probing like a Worm-eating Warbler (*Helmitheros vermivorus*) (see Norris, *op. cit.*) in clusters of dead leaves in subterminal and terminal parts of bush or tree branches, or in the axil of a cane (*Arundinaria*) plant a few feet above the ground. It is similarly attracted to a cluster of debris washed up against the base of a group of sapling stems following the flooding of the bottomland forest. Occasionally I have observed the Swainson's Warbler leave a perch in pursuit of a flying insect.

The bill of the Swainson's Warbler is larger and more sharply pointed than the bills of the Ovenbird (*Seiurus aurocapillus*), Louisiana Waterthrush (*Seiurus motacilla*), and Kentucky Warbler (*Oporornis formosus*), ground feeding parulids that obtain their food primarily from the surface of the leaf litter and from other components of the forest floor.

The Kentucky Warbler hops along flushing insects, picking them off stems and from leaves of low-growing vegetation, and probing into crevices among leaves and sticks. The Ovenbird, a walker, feeds similarly but more in the open, as does the waterthrush, also a walker, which feeds about wet leaf litter along streams and in shallow pools. The waterthrush does some leaf flipping in contrast to the leaf-shoving and tilting of the Swainson's Warbler.—BROOKE MEANLEY, *U.S. Department of the Interior, Patuxent Wildlife Research Center, Laurel, Maryland 20810, 8 July 1969.*

Rufous-crowned Tanagers feeding on fruitbowl.—Hundley and Mason (*Wilson Bull.*, 77:408, 1965) mention a number of bird species feeding on fruitbowl in the West Indies. On 14 November 1950 I observed a couple of Rufous-crowned Tanagers (*Tangara cayana*) feeding on fruitbowl on a dish in the dining room of a hotel in Georgetown, Guyana. This behavior came as a surprise to me as in neighboring Surinam this species is not a town dweller but is confined to the sandy savannas as stated in my “Birds of Surinam” (1968. Oliver and Boyd, Edinburgh).—F. HAVERSCHEIDT, *Wolfskuilstraat 16, Ommen, Holland, 29 March 1969.*

ORNITHOLOGICAL NEWS

Olin Sewall Pettingill, Jr. has retired from the position of Ornithological Literature Editor of the *Bulletin*. Dr. Pettingill has served in this capacity since 1959, and to him goes most of the credit for the development of the "Ornithological Literature" section into the lively and interesting feature it has become. The new Ornithological Review Editor is Dr. Peter Stettenheim of Plainfield, New Hampshire.

The large backlog of papers awaiting publication combined with the limited funds available have made it impossible to publish a list of the recent accessions to the Josselyn Van Tyne Memorial Library. Members who are interested in list B-8 which contains the additions since the publication of the list in 1965 may obtain a copy by writing to the Van Tyne Library, Museum of Zoology, University of Michigan, Ann Arbor.

Dr. Loye H. Miller, a member of the Wilson Society since 1939 died on 6 April 1970 in his ninety-fifth year. Besides his work as an avian paleontologist Dr. Miller will long be remembered as an inspiring teacher, and as one of the founders of the interpretive naturalist program in the National Park Service.

In order to clear up the confusion that has arisen concerning the identification of the geese in the frontispiece to the March 1970 issue of *The Bulletin*, Dr. Ryder has supplied the following information.

In the frontispiece entitled, "Ross' Geese (*Chen rossii*) nesting on an island at Karrak Lake, Northwest Territories, 24 June 1967," the two geese "resting" at the extreme left of the picture are Lesser Snow Geese. The bird standing in the center is a male Lesser Snow Goose with his mate incubating beside him. The goose "walking out" of the frontispiece at the right is a Lesser Snow Goose. Two Ross' Geese are seen in the foreground, the male standing and the female incubating.

Dr. Helmut C. Mueller of the University of North Carolina is the newest member of the Editorial Board of *The Bulletin*.

In my study on the systematics of the five subspecies of White-tailed Ptarmigan, I have examined over 600 specimens in the major museums. I have found that populations from Colorado, Alberta and mainland British Columbia are well represented in museums. However, populations occurring in Alaska, Yukon and adjacent Mackenzie District, N.W.T., Montana, Idaho, Washington, Wyoming, New Mexico, and Vancouver Island are not well represented in museum collections. I would be grateful to learn of specimens from these areas deposited in museums or collections that I have not previously contacted. Please send information to Dr. Clait E. Braun, Game Research Center, P. O. Box 567, Fort Collins, Colorado 80521.—C.E.B.

ORNITHOLOGICAL LITERATURE

EAGLES, HAWKS AND FALCONS OF THE WORLD. By Leslie Brown and Dean Amadon. McGraw-Hill Book Co., New York. 1968: 2 vols. (boxed), $8\frac{3}{4} \times 11\frac{1}{4}$ in., 945 pp., 165 pl. (125 in color), plus 15 under-wing pl., 94 range maps, ~~33 text figs.~~ \$59.50.

Confronted with a book listing at \$59.50, the reader of a review of that book is interested *primarily* in the answer to one question: "Is it worth it?" In the case of "Eagles, hawks and falcons of the world," this reviewer must reluctantly answer "No." At the same time, I must also say that it is an important and valuable book, and that my library would be incomplete without it. This is not the paradox it may seem. Remember that the initial question dealt with the *price*. I was fortunate enough to receive a *gratis* review copy. Had I paid about sixty dollars for it, I would, after having examined it for any length of time, have felt that I had been cheated. This is a strong statement, and will, of course, be explained.

Documentation of the faults of the book will, of necessity, occupy most of the space devoted to this review, simply because a reviewer is seldom challenged for documentation to support a *favorable* statement, whereas the basis for *negative* criticism must be demonstrated. Therefore let me reiterate at the outset that this is a very important book. Both authors have devoted long hours of field work to the study of the diurnal birds of prey; the senior author has virtually made this study his career. The junior author has had at hand the superb collections in the American Museum of Natural History, supplemented with material from other museums; the detailed descriptions show how carefully these specimens have been studied. A tremendous body of literature has been consulted and, in general, successfully summarized. The illustrations, descriptions, and range maps will be extremely useful to anyone wishing to identify the often difficult species in this group. The museum curator can use the book in his office but it is far too massive to use in the field. The organization of the book, however, will permit a traveler to study in advance the species he is likely to see wherever he goes; a synopsis of field characters of genera, for example, is grouped into major geographic regions. The first several chapters (through p. 150) constitute a good general introduction to the birds of prey and their biology. Unfortunately the long delay in publication did not permit inclusion of some of the more recent findings on the effects of pesticides on birds of prey. A conservationist in 1970 will probably consider this topic underemphasized in the book. In the chapter entitled "Longevity, mortality and enemies," about 50 per cent more space is allotted to the hazards of motor cars than to those of pesticides.

Throughout the book the authors have made a special effort to point out gaps in our knowledge, and have suggested specific projects worthy of study. These include such widely disparate subjects as the aerodynamics of the Bateleur and the eye anatomy of snake-eagles. For a potential graduate student interested in the birds of prey, the present book is a treasurehouse of possible thesis problems.

Finally, thanks to the set of plates in this book, the Falconiformes can rank near the Anatidae among the most thoroughly illustrated of major groups of birds. Every species, many subspecies, and many age, sex, and color-phase variants are shown either in color or half-tone. Subject to the qualifications to be mentioned beyond, these plates will be exceedingly useful.

It must be stated immediately that many of the faults of the book are as disturbing to the authors as they are to a reader. During the production of the book Brown worked in Africa, Amadon in the United States. Country Life, the English publisher with which the

original contract had been signed, was purchased by the Hamlyn Publishing group midway in the project, and the authors found themselves dealing with a completely changed editorial personnel. The book's actual publication after completion of the manuscript was long delayed during negotiations with American publishers, and a trip to England Brown made specifically to be on hand when the book went to press failed of its objective. The plate captions, the legends for the maps, the terminal bibliography, and the index were all printed without proofs having been submitted to either author. These portions of the book are riddled with errors.

For the facts in the preceding paragraph, I am indebted to a four-page errata supplement; this is available upon request from Dr. Amadon's office at the American Museum of Natural History.

Even a spot-check of the plate captions indicates that all of the errors and discrepancies were not listed on the errata sheets. In some species described in the text as sexually dimorphic, the plate figure is simply labeled "adult" (cf. *Aviceda cuculoides*, pl. 6). On the other hand, no sexual dimorphism is described for the Osprey, yet two very different-looking birds are captioned "adult male" and "adult female" of *Pandion h. haliaetus* in pl. 5. From its characters, I suspect that the "adult male" was intended to portray the North American subspecies, *P. h. carolinensis*. Judging from the text descriptions (see especially the number of tail bars), the captions have been reversed for the adult and immature of *Aviceda madagascariensis* on pl. 6. And so on.

The main text is by no means free of typographical errors: "Columbia" (twice) for Colombia on p. 192; "*Harpiopsis*" for *Harpyopsis* on p. 24; "G. S. Sutton" for G. M. Sutton on pp. 255 and 258, etc. Most such misprints are obvious and harmless (unless there are similar misprints in numbers, such as measurements or literature citations; I have not checked these), but the errors in captioning can be serious and misleading. As mentioned earlier, the authors were unable to proofread these.

Also beyond the control of the authors is the one flaw of the book that does the most to justify my statement that it is not worth the price. I refer to the reproduction of the color plates. I thought of several extremely vivid deprecatory adjectives to apply to the color reproduction in this book, but settled on "inexcusable." When a publisher asks sixty dollars for a book, and then delivers plates that are travesties of the original paintings, one might almost invoke the word "fraud." A potential purchaser *might* be able to thumb through several copies, if available at his bookstore, and pick the "least worst" of the plates; there is inconsistency from copy to copy. One belonging to a colleague has been compared with the review copy; the latter averages much worse.

What the plates *could* have, and *should* have, looked like may be ascertained by examining the issues of *Audubon* magazine for September–October and November–December 1968. Seven of the book's color plates were reproduced in the first issue, and eight (all of vultures) in the second. I do not know the size of the press run of *Audubon*, but it is certainly mass-produced. Les Line, the magazine's editor, has assured me that the plates in the magazine were printed from the same engravings as used in the book. Two of the eight artists have told me that the color *proofs* they received were excellent, and up to the quality of the plates reproduced in *Audubon*. That the publishers permitted this book, obviously a luxury item, to be sold with the quality of color reproduction found in the "finished" version is thus all the more inexcusable. It is not primarily a matter of register, a common fault in color reproduction; none of the plates in my copy is *grossly* off register (as, for example, are some of the plates in another recent expensive book, "Birds of Colorado" by Bailey and Niedrach, 1965). The problem is in the colors them-

selves. When compared with their counterparts in *Audubon*, the plates in the book are seen to be muddy, uncrisp, and inaccurate—generally washed over with reddish tones. The pale buff underparts of the Laughing Falcon (p. 134), for example, have become a sort of sickly orange brown. Roger Peterson's vulture plates, which several people have told me they consider to be among his finest work (I disagree, but that is a subjective judgment), have perhaps suffered the worst. One *must* look at the reproductions in *Audubon* to see what Peterson was really trying to do in these paintings.

Under such circumstances, a reviewer usually expresses the hope that a second printing or second edition will have better color reproduction. For a potential buyer of the book who is chiefly interested in the plates, it can only be hoped that the first printing will sell out to readers who need to have the textual material available, and for whom the plates are of secondary importance. Otherwise there probably won't *be* a second printing.

While on the subject of the plates, a word on the artists is in order. Three are British: J. C. Harrison, represented by 70 plates; C. E. Talbot Kelly, with 15; and David Reid-Henry, with 10. The five Americans are Don R. Eckelberry (29 plates), Albert E. Gilbert (21), Roger T. Peterson (10), Guy Coheleach (7), and Lloyd Sandford (3)—these are hasty plate counts of my own, and I do not guarantee their accuracy! Several distinct painting styles are represented, and tastes will certainly differ as to their aesthetic qualities as well as their success in portraying a given species of bird. I am sure, however, that few will deny that Reid-Henry's plates (especially the falcons) and those of Eckelberry represent these superior bird-painters at their finest, or that Gilbert is rapidly proving himself to be a worthy apprentice to the masters.

At the end of the first volume, 15 field-guide style "under-wing" plates are grouped geographically, a useful arrangement. The field observer who wishes to identify a soaring hawk, however, had best be sure to take good notes or make his own sketches, as he is not likely to want to carry the book with him. Volume 1 alone weighs five pounds two ounces, and both volumes plus slipcase weigh twelve pounds six ounces (weights courtesy of our local postmistress).

One matter remains to be mentioned in connection with the illustrations. The introduction (p. 12) states: "A problem with many birds of prey is the sub-adult plumage or plumages. We have not attempted to illustrate these, as they are little understood and, in all but a few instances, are more or less obviously intermediate between the first immature and the adult dress." This seems to me to be a little defeatist, especially as birds in such plumages are rather frequently encountered in the field, and may present puzzling problems in identification. Obviously space would not permit the illustration of all or even most transitional plumages. But whether or not their sequence is "understood," at least these plumages are identifiable as to species, and could be portrayed. It does seem somewhat arbitrary, for example, to illustrate *one* "immature" plumage for birds such as the California Condor or the Bald Eagle, in which as many as five to seven age-classes may be distinguishable. In the plate of the King Vulture (pl. 2), the plumage shown is allegedly that of the "first immature," but the figure as painted combines the plumage of a first-year bird with the head colors of a bird at least two years old. Only adults of *Circus cyaneus*, *macrourus* and *pygargus* are figured, although young birds are by no means identical in appearance to the adult females. Pl. 11 shows the "immature" of *Henicopernis infuscata* as radically different from the adult, but the text (p. 219) simply describes the adult of this species and then states "Immature probably little different."

Turning now to the text, throughout the book and especially in the species accounts the reader is gratifyingly conscious of the fact that this is no mere compilation. Page

after page is filled with information, often hitherto unpublished, based on the authors' own field experience with birds of prey all over the world. One need only contrast the perfunctory accounts of some of the little known (even if widely distributed) species, such as *Leucopternis* sp., with the lively and detailed first-hand accounts of, say, *Buteo galapagoensis* or *Aquila wahlbergi*, to appreciate the value of so much of this book.

The writing is generally readable, although marred by occasional grammatical lapses irritating chiefly to pedants like the reviewer. The authors are addicted to long sentences formed of a string of comma-bordered phrases. On p. 148, for example, I found a 62-word sentence immediately followed by a 57-word sentence. The reader may be pardoned if he occasionally gets lost in such labyrinths.

One sentence on p. 63 is truly of *Auklet* quality: Bald Eagles in Florida "begin nesting not merely early in the year, but in the autumn of the preceding year. . ." In other words, they don't nest this year, they nest last year. Shades of Lewis Carroll!

The subject matter of the introductory chapters naturally duplicates to some extent that in the species accounts, and even in the introductory chapters themselves there is overlap (feeding habits and adaptations are mentioned, for example, in most of these chapters). Some repetition is therefore inevitable, but it does seem a bit redundant to find a peculiar habit of the New Zealand Harrier (discontinuing incubation while there are still fertile unhatched eggs in the nest) mentioned on pp. 108, 109, 111, 127, and in the species account on p. 386.

I have generally understood "fledging" to mean the acquiring of flight feathers and consequently of flight in young birds. Brown and Amadon consistently use "fledging period" to mean the time commencing at hatching for which most authors tend to use "nestling period."

In a compendium of this size, any specialist can find what he would consider errors, both of omission and commission. This could hardly be avoided without asking the authors to devote a lifetime to writing the book, and to correspond with everybody who has ever looked seriously at birds of prey. Such points can be called to the attention of the authors for possible use in a new edition or supplement; in the errata pages mentioned above, there are already several corrections submitted by readers (Eisenmann on soft-part colors of *Cathartes* sp., for example). As a sample of the kind of thing I mean, I noted that the descriptions of the subspecies of the Osprey are rather misleading. The head of the Australian forms is not "pure white," as the broad dark band is present on the sides of the face, scarcely less prominently than in the North American race *carolinensis*. On the other hand, the Caribbean race *ridgwayi* (which is erroneously stated on p. 153 to be confined as a breeding bird to the Bahamas), characterized by Brown and Amadon by its smaller size and white breast only, is *truly* white-headed; the traces of brown on the crown and ear coverts are, at most, barely visible in the field.

As an example of omission, I was surprised to find no bibliographic mention of the article "Falconry, the sport of kings," superbly written and illustrated (in color and black-and-white) by Louis Agassiz Fuertes, in the December 1920 *National Geographic Magazine*. I have seen no finer paintings of birds of prey *in action* than those by Fuertes.

Much of the above criticism of the text is of relatively little moment in proportion to the overall importance of the book. There *is* one aspect of the text, however, that I would score as a serious fault. I refer to the documentation, both with respect to the presence and absence of references, and to the nature and placement of these when present. Bibliographic citations in this book are of several kinds. So-called "references" are placed at the ends of some (but not all) of the introductory chapters. These generally represent

the documentation for some (but again, not all) of the statements credited by name to other authors in that particular chapter. The "supplementary bibliography" at the end of volume 2 is arranged by chapters, and *some* of the papers or books referred to in the text but not listed at the end of the chapter are listed in this bibliography. Nevertheless, I constantly came across authors mentioned by name whose papers or books were listed in *neither* bibliography; examples are Tinbergen (p. 27), Cade (p. 39), Munro (p. 49), etc. Similarly, references are given at the ends of species accounts to some but not all of the authors cited by name. This is frustrating to the reader who may wish to pursue a subject in more detail. All of the book with the exception of that part based on the authors' own studies may be considered to be a compilation from earlier literature, and the authors themselves have stated that they cannot possibly document every statement. The use of authors' names without references to their works, therefore, becomes a space-consuming "pseudo-documentation."

In what is apparently a misguided attempt to be concise, most of the literature citations at the ends of chapters have been greatly truncated, although utterly inconsistently and to the detriment of their usefulness. Thus, in the references at the end of chapter 6, two papers in *The Ibis* are cited with volume number, year, full title of paper, and inclusive page numbers. For one paper in the *Journal für Ornithologie* the title of the paper is omitted; for one in *The Wilson Bulletin* the volume number and pagination are omitted. This has not accomplished much in the way of space-saving, as virtually all of the chapters (including 6) end with about half a page of blank space.

Throughout the book I found intriguing statements with *no* documentation, statements whose origin I would have liked to know, such as the suggestion on p. 47 that small birds "may show much more concern about the presence of a lean and hungry hawk than a well-fed one." Sometimes a little patience and a little detective work helps. On p. 17 we learn that "new anatomical findings indicate that the owls may be related after all, though distantly, to the diurnal birds of prey, or at least to the falcons." Since this statement is in disagreement with what we have always been taught, we are immediately interested. However, there is no indication at this point as to what, or whose anatomical findings are involved. On p. 23 we learn of the work of Starck and Barnikol, who have shown "that the musculature of the head of a falcon is more like that of an owl than a hawk." Would it have taken much more space to say *which* falcon, owl and hawk? In this instance, the title of the paper happens to be cited in the references at the end of the chapter, and we see that the paper by Starck and Barnikol deals only with "Morphologie der Trigemini-muskulatur. . ." One might have expected that the generalization about "new anatomical findings" and relationships given on p. 17 would be somewhat more broadly based, but apparently it is not.

On p. 35 there is a parenthetical reference to "(Brown, *Eagles*)" in a discussion of immature plumages. One looks in vain for a more complete bibliographic citation of Mr. Brown's book either at the end of chapter 3 (where there are *no* references) or in the portion of the terminal bibliography devoted to references pertaining to chapter 3. Again, a little patient detective work pays off, and we find the citation in the second portion of this bibliography, which is arranged by groups of birds, under "eagles." The allocation of references in the bibliography is often unpredictable and detracts from its potential usefulness. For example, as there is no general chapter on anatomy, one might expect to find Berger's paper on the appendicular myology of the Pygmy Falcon listed under "falcons, caracaras," but it is not; it is listed among the references for chapter 1, "classification and distribution" (as are, also, specialized papers on the systematic position of

Gampsonyx and of *Heterospizias*). A paper by Clay on "protective coloration" in *Falco sparverius* is not listed among the references at the end of the species account, nor among the papers in the bibliography pertaining to falcons, but under chapter 3, "plumages and moults." In short, although the number of books and papers cited in one way or another in all parts of the book combined is phenomenal, the usefulness of the documentation is severely impaired by its incompleteness and difficulty of access.

In a book review by a taxonomist, the reader expects to find at least a few remarks on the taxonomy of the authors. Their approach to classification is, by and large, quite "middle-of-the-road." They acknowledge having been influenced by an unpublished manuscript prepared by Erwin Stresemann for a proposed revision of volume 1 of Peters' "Check-list" and loaned by him to Brown and Amadon. As the latter admit, full evaluation of Stresemann's classification (and departures from it made by Brown and Amadon) is not possible until the list has been published. The authors are outspoken in their dislike of name changes for purely nomenclatorial reasons, and have therefore retained certain names, such as *Polyborus* and *Circus buffoni*, that have been altered in some recent publications. Any taxonomist is bound to disagree with at least an occasional taxonomic decision made by Brown and Amadon. For example, in view of some other "lumpings" I cannot see the justification for admitting four rather than two species of *Elanus* (see Parkes, *Condor*, 60: 139-140, 1958 and Husain, *Condor*, 61: 153-154, 1959); Brown and Amadon's "discussion" on this point is confined to a statement (p. 236) that *E. leucurus*, *caeruleus*, and *notatus* are "usually and probably correctly considered to comprise three species."

But some such disagreements are, as I say, inevitable, and I roundly applaud the care with which Brown and Amadon have acknowledged (especially in a series of tables on pp. 160-162) taxonomic and nomenclatorial usages other than those they have elected to follow in their book.

In summary, "Eagles, hawks and falcons of the world" is a major accomplishment, and a book that belongs in all institutional libraries. Purchase by individuals out of their own pockets must depend upon the significance to the potential purchaser of the book's several serious flaws (many the fault of neither the authors nor the artists) in relation to the very high price.—KENNETH C. PARKES.

BIRD SONG: ACOUSTICS AND PHYSIOLOGY. By Crawford H. Greenewalt. Smithsonian Institution Press. Washington, D.C. 1968: 8 × 11 in., 194 pp., 168 figs., 23 tables, 2 7-in. records, 33½ r.p.m. \$12.50.

HOW BIRDS SING. By Crawford H. Greenewalt. *Scientific American*, 221: No. 5, Nov. 1969: pp. 126-139, 7 plates, 14 figs., 9 bl. and wh. illus.

How do birds sing? Why is it that for so long no firm bridge has been found across the gap from the anatomist's precise description of the avian syrinx to a lucid interpretation of how it functions in the production of sound?

Crawford Greenewalt's study seems to make this point: the answer to how birds sing is a complex one to be reached only through an interdisciplinary approach that includes elements of animal behavior, anatomy, physiology, physics, and acoustical, electrical, and mechanical engineering.

Dr. Greenewalt's distinguished career is in chemical engineering, and therefore not precisely in any of the above fields. Once motivated to tackle the problem, however, he was able to muster an impressive array of resources: a sharply analytical mind, the training and background of scientific research, ready access to the best technical advice and tech-

nical equipment, and, not least, an abiding interest in the behavior and physiological functioning of birds.

He chose not to use laboratory research with the living bird; instead, he has based his case on deductive reasoning derived from an examination of the amplitudes and frequencies of bird sounds, as measured and portrayed by the oscilloscope, sound spectrograph, wave analyzer, and a range of frequency filters. He has then interpreted these results in the light of the best available descriptions in the literature of the avian syrinx, trachea, and associated structures.

His conclusions are stated as succinctly as possible in one paragraph of the article in *Scientific American*, which I quote:

“Let me summarize. The physiology and acoustics of bird vocalization are unique in the animal kingdom. Sound is produced at the syrinx in an air stream modulated by an elastic membrane vibrating in a restricted passage bounded by the walls of the bronchus. This source-generated acoustical disturbance appears not to be modified in its passage through the trachea. The syrinx contains two independently controllable sources, one in each bronchus, enabling the bird to produce two notes or phrases simultaneously. Harmonics arise below a threshold frequency by mechanical constraints on the vibrating membrane, forcing a departure from a purely sinusoidal wave form. The source-generated sounds can be modulated in frequency or in amplitude or (more usually) in both with extraordinary rapidity, so rapidly that human ears cannot perceive the modulators as such, receiving instead impressions of notes of varying quality or timbre.”

Each of these conclusions has a chapter devoted to it in the book. Preliminary chapters deal with instrumentation (particularly valuable for anyone contemplating electronic analysis of bird sounds) and the anatomy of the syrinx. Chapter 4, entitled “A Portfolio of Whistled Song,” is primarily a series of plates showing examples of oscillograms and corresponding sonograms of sounds of 60 species chosen mostly at random. The text includes provocative definitions of both “whistled” and “song” that nevertheless seem logical and acceptable. Sonograms are lacking for Great Gray Owl, Horned Lark, Carolina Chickadee, and a portion of the Red-winged Blackbird—perhaps because they failed to print. Two records in the back of the book illustrate these recordings and other plates in subsequent chapters. Their primary value is in the slowed-down versions that enable the sonograms to be followed note for note; they also illustrate the components of “the two acoustical sources” (chap. 5). Among the plates in this chapter, I expected to find examples from that exceptionally talented singer, the Hermit Thrush. Alas, although the Wood Thrush has four plates and the Gray-cheeked Thrush one, there are none for the Hermit.

Undoubtedly the most surprising conclusion in the book is that the trachea does not modify sound produced by the syrinx. If not, then how can one explain the intricate development of the trachea in the Trumpeter Swan or Whooping Crane, for instance?

The author postulates that if the ratio of the cross-sectional area of the trachea to that of the syrinx is in the general order of ten to one, then resonance is dampened and harmonics rarely occur in the trachea. He believes that in fact this ratio does exist in most birds, though supporting evidence is rather thin. However, convolution in the trachea of the Trumpeter Swan remains unexplained in the evolutionary sense of contributing to survival value. Perhaps the most telling support for a non-resonating trachea is that the dual sound sources thereby maintain their individuality instead of being subject to modification in a combined form.

Two other general conclusions reached by the author are worthy of note: (a) there seems to be no consistent relationship between sound frequency in the song and the size

of the bird; (b) songs show no strong simplicity relationship in the evolutionary trend from loon to longspur.

The general style of prose is clear and concise, but the reader is required to exercise his brain at a fairly high level of intensity and he is assumed to have a well-based scientific and mathematical background.

The article in *Scientific American* is composed largely of sizeable extracts of key portions of the book. There are of course many fewer illustrations, but those which are reproduced are more clearly labelled and easier to comprehend. A schematic diagram of the relevant air sacs of a bird makes a worthwhile addition. The article is recommended for those who are interested in the subject but have only an hour or so to devote to it. Those with a more compelling interest will find the book challenging but rewarding. It is an important contribution to ornithology that perhaps only the author could have made. He is the first to say that he may not have the final answers, but he is to be congratulated on having established a solid edifice that may only be challenged or extended through actual laboratory experimentation on birds.—WILLIAM W. H. GUNN.

PHYSIOLOGICAL SYSTEMS IN SEMIARID ENVIRONMENTS. Edited by C. Clayton Hoff and Marvin L. Riedesel. University of New Mexico Press, Albuquerque, 1969: 6 × 9½ in., xi + 293 pp., many figs. \$9.00.

This publication deals with an ambitious seminar conceived and organized by Marvin L. Riedesel. The seminar suffered from the compromise funding which has characterized so much of recent NSF decisions—not enough money to really do it right, but just enough to keep it going. The title is somewhat misleading in that the various reports deal with both desert and semidesert environments. Some of the reports are obviously inappropriate, e.g., “Multiple Hypothermic Experiences in Infant Albino Rats” or “Oxygen Consumption by Fluoride-inhibited Bat and Rat Heart Homogenates.” They may serve to illustrate the stated objectives of demonstrating the importance of conducting studies at various levels of organization, but they are inappropriate examples for a seminar on desert and semidesert adaptations. The papers have not been subjected to the rigorous editing found in most scientific journals. As a result, procedures such as the use of Schultheis thermometers to obtain rectal body temperatures on 3.5 gram bats, a technique inappropriate for accurate determination of deep body temperature, are tolerated.

The seminar carries a strange mixture of regional, continental, and world-wide approach to the study of physiological systems. No doubt this is a consequence of limited funding and the extent to which cooperation from established investigators could be obtained.

A number of papers are without scholarly documentation and include such statements as “In years with abundant seed production rodent and ant populations increase very much, but decline again in poor seed years.” This sort of statement has profound ecological implications and should either be documented or properly referenced. Statements such as “Well integrated research may reveal a number of unknown relationships between man or other animals and the atmospheric environment of arid and semiarid regions” sound impressive, but are meaningless.

Some of the review papers fell far short of their mark and might better have been left out because they are poor examples of scholarship. The failure of some of the participants to provide more than an abstract detracts seriously from the value of this publication. On the other hand, the editors are to be commended for having avoided unnecessary delay in the publication of this seminar in by-passing laggards.

In the overall evaluation of this publication it is necessary to note with care what it was

intended to be, *viz.*, (1) a device for stimulating research, (2) to further integration of research and teaching programs in colleges located in and near semiarid areas, and (3) to facilitate communication among investigators and students located within the southwestern region. These objectives are obviously regional in perspective and were fairly well achieved. As an authoritative source of information about arid environments, the publication is inadequate. However, if it is used eclectically and with some prior insights, there is much useful and stimulating information contained in it.—J. W. HUDSON.

FRANK M. CHAPMAN IN FLORIDA: HIS JOURNALS AND LETTERS. Compiled and edited by Elizabeth S. Austin. University of Florida Press, Gainesville, 1967: 6 × 9¼ in., x + 228 pp., 6 photos. \$7.95.

Frank Michler Chapman spent a part of almost every winter in Florida, beginning in 1886 when he was 22 years old. In the early years he worked in the Gainesville area; later he ventured farther afield—to the Suwannee River, the Dry Tortugas, and the Everglades—always collecting birds for the American Museum of Natural History. After 1932 he lived quietly on the shore of Biscayne Bay where “. . . he did not go exploring in the wild country and bring new birds and mammals to his beloved museum. . . .” Rather, “. . . he planned a season of discovery among familiar creatures in his own back yard.” While in Florida he kept a journal of his daily activities and, in the earlier years, frequently reported to his superior at the American Museum, Joel Asaph Allen, in long informal letters.

Elizabeth Austin deserves high praise for assembling the material and weaving it into a delightful story of this little-known segment of Frank Chapman's life. Dr. Chapman never neglected the people he met and the places he visited and neither does she. Historians will thank her for the revealing picture of Gainesville in the 80's. Probably no better record exists. Although the collecting, reading, and selecting of passages must have been time-consuming and often tedious, the finished work gives no hint. The writing is lively, its spirit as enthusiastic as was the man himself—even in his later years.

Each ornithologist will have his own reaction: Graybeards will try to relate the 22-year-old, who gave up banking for birds, to the vivacious old gentleman attending his last A.O.U. meeting; those in the middle years will remember *Bird-Lore*, founded, edited, and often illustrated with photographs by Chapman; the young, to whom the name means essentially a grant from the American Museum, may be surprised to learn that Chapman was an ecologist and ethologist long before they were born. The bibliography of his work, complete except for book reviews, notes, and editorials in *Bird-Lore*, includes 19 books and over 300 articles, staggering in both length and variety—from “Birds and Bonnets” (*Field and Stream*, 1886) to “Description of the Nestling Plumage of *Falco islandus*” (*Auk*, 1900), and from “Hunting with a Camera” (*World's Work*, 1903) to “Everglade Islet” (*Audubon Magazine*, 1943). The fact that he accomplished so much in an era when communication and traveling were far more difficult than at present should cause each of us to wonder what we do with our time.

The last chapter, “Birds of the Gainesville Region, Then and Now,” by Oliver L. Austin, Jr., reveals the changes in birdlife following the cutting of vegetation and draining of swamps to make room for the growing town. The addition of 93 species to Dr. Chapman's original list of 149 species for Alachua County shows that the spark provided by Chapman continues to flourish in Florida today.

Frank M. Chapman recognized no boundaries between professional and amateur ornithologists and neither does this book. All will enjoy it.—ELEANOR RICE PETTINGILL.

THE WORLD OF THE CANADA GOOSE. By Joc Van Wormer. J. B. Lippincott Company, Philadelphia, 1968: $7\frac{3}{4} \times 10\frac{1}{4}$ in., 1922 pp., illus. \$5.95.

This would appear to be just another book on the Canada Goose except that it was written for the layman instead of the ornithologist or the wildlife manager. It is similar to "Honker" by C. S. Williams (D. Van Nostrand, 1967) in subject and content, but is less scholarly. "The World of the Canada Goose" is the 15th book in the Living World Books series edited by John K. Terres. It is the third dealing with a bird species, and the fourth in the series by this author. It is not the best in the series. The author has done his homework in researching this book but does not show a broad familiarity with birds or with this species.

Some of his information borders on the inaccurate. The Canada Goose does not have red flight muscles because of the large number of blood vessels (p. 30) so much as because of the great quantity of myoglobin in the tissue. The supposition that there is much loss of very young goslings to internal parasites (p. 146) belies the time necessary to develop heavy infections of most parasites. I doubt if the author really meant to refer to ducks and geese as "two species" (p. 105), or to three races of the Canada Goose as species (p. 172). He appears unsure of the present and historic status of the Canada Goose when the reader compares statements on page 108 with those on pages 129 and 157.

While it may improve readability, it does not increase my confidence to be informed that since . . . "the Canada is an eminently practical bird it does not expend energy foolishly" (p. 121). I fail to understand how the preference of older geese for a previously occupied territory "induces territorialism" (p. 46), or how one would recognize a goose that is "happy in the knowledge" that it has exerted dominance over a resident pair (p. 47).

The book is illustrated with many pictures by the author, most of them excellent, but I do not understand why a picture of a flock of Sandhill Cranes appears on page 122 when there is no mention of the species anywhere that I could find.—JAMES TATE, JR.

PUBLICATION NOTES AND NOTICES

BANKERS, BONES, AND BEETLES: The First Century of the American Museum of Natural History. By Geoffrey Hellman. Natural History Press, Garden City, New York, 1969: $5\frac{1}{2} \times 8\frac{1}{2}$ in., 275 pp., 18 photos. \$5.95.

From the book's jacket: "Written with wit and affectionate irreverence by Geoffrey Hellman, this book is an anecdotal history of the remarkable men—financiers, scientists, philanthropists, and eccentrics—who have been associated with the greatest natural history museum in the world. But, chiefly, it is a celebration of the growth of a renowned institution, repository for 16,000,000 mammals, minerals, meteorites, fossils, fish, insects and birds, and lodestar to 3,000,000 visitors a year."

COLLECTED PAPERS IN HONOR OF LYNDON LANE HARGRAVE. Edited by Albert H. Schroeder. Museum of New Mexico Press, Santa Fe, 1968: 6×9 in., paper covered, 169 pp. No price given.

Among the ten papers are the following four of ornithological import:

Birds and Feathers in Documents Relating to Indians of the Southwest (pp. 95–114).
Albert H. Schroeder.

Limb Measurements of the Extinct Vulture, *Coragyps occidentalis*: With a Description of a New Subspecies (pp. 115–128). Hildegarde Howard.

The Instability of the Distribution of Land Birds in the Southwest (pp. 129–162). Allan R. Phillips.

A Hairy Woodpecker from Petrified Forest National Park, Arizona (pp. 163–164). Norman G. Messinger.

SONGBIRDS IN YOUR GARDEN. By John K. Terres. New expanded edition. Thomas Y. Crowell Company, New York, 1968: $6\frac{3}{4} \times 9\frac{1}{2}$ in., xvi + 256 pp., illus. with line drawings by Matthew Kalmenoff. \$6.95.

This is a thorough revision of the original edition published in 1953. Besides a larger format with many new line drawings and an updating of all information, the new edition features an additional chapter on how to build a bluebird trail. "Songbirds in Your Garden" is essentially a guide to attracting birds about the home, but includes many first-person anecdotes by the author, thus making it highly readable as well as instructive.—O.S.P.

ANIMAL COMMUNICATION: TECHNIQUES OF STUDY AND RESULTS OF RESEARCH. Edited by Thomas A. Sebeok. Indiana University Press, Bloomington, 1968: $6\frac{1}{4} \times 9\frac{1}{2}$ in., xviii + 686 pp., many figs. \$20.00.

From the book's jacket: "Twenty-four original articles by world-renowned experts in the fields of zoology and psychology present an extensive survey of the 'state of the art' as of the late 1960's." The articles are grouped under five headings: Introduction (one article by the editor), Techniques of Study (four articles), Some Mechanisms of Communication (four articles), Communication in Selected Groups (nine articles), Implications and Applications (six articles). The article on birds by Barbara I. Hooker, a graduate student at New Hall College, Cambridge, is restricted to vocal communication and is essentially a brief review of the subject.

This issue of *The Wilson Bulletin* was published on 5 June 1970.

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

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CONTENTS

- THE NESTING ECOLOGY AND REPRODUCTIVE PERFORMANCE OF THE
EASTERN MEADOWLARK *John L. Roseberry and W. D. Klimstra* 243
- DOMINANCE-SUBORDINATION IN CAGED GROUPS OF HOUSE SPARROWS
John R. Watson 268
- AVIAN BILL-WIPING *George A. Clark, Jr.* 279
- EGG TEETH AND HATCHING METHODS IN SOME ALCIDS
Spencer G. Sealy 289
- GROWTH RATES AND SEX RATIOS OF RED-WINGED BLACKBIRD
NESTLINGS *Larry C. Holcomb and Gilbert Twiest* 294
- COWBIRD PARASITISM AND NESTING SUCCESS OF LARK SPARROWS IN
SOUTHERN OKLAHOMA *George A. Newman* 304
- DUST-BATHING SITES SELECTED BY RUFFED GROUSE *Dale Hein* 310
- OBSERVATIONS OF THE BREEDING BIOLOGY OF THE VERMILION
FLYCATCHER IN ARIZONA
Walter Kingsley Taylor and Hugh Hanson 315
- GENERAL NOTES
- ADDITIONAL NOTES ON THE PLUMAGES OF THE REDHEAD (*AYTHYA AMERICANA*)
Milton W. Weller 320
- OBSERVATIONS ON PREMIGRATORY MOVEMENTS OF HAND-REARED MALLARDS
James J. Zohrer 323
- TRUMPETER SWAN CARRYING YOUNG *Donald A. Hammer* 324
- NOTES ON THE FOODS OF JUVENILE BLACK-BELLIED TREE DUCKS
Eric G. Bolen and John J. Beecham 325
- SUCCESSFUL RECONSTRUCTION OF ACTIVE BALD EAGLE NEST
Thomas C. Dunstan and Melvin Borth 326
- TERRITORIAL CONFLICT IN THE AMERICAN WOODCOCK *Frederic W. Davis* 327

CHUCK-WILL'S-WIDOW IN CONNECTICUT	<i>Eugene S. Morton</i>	329
PREDATION OF A BLACK RAT SNAKE ON YELLOW-SHAFTED FLICKER NESTLINGS	<i>Jerome A. Jackson</i>	329
WING FLASHING IN A BROWN THRASHER AND CATBIRD	<i>Edwin D. Michael</i>	330
RE-EVALUATION OF TWO SUPPOSED HYBRID BIRDS	<i>Richard C. Banks</i>	331
THE AVIFAUNA OF THE SAND DRAW LOCAL FAUNA (AFTONIAN) OF BROWN COUNTY, NEBRASKA	<i>J. Alan Feduccia</i>	332
ORNITHOLOGICAL NEWS		335
ORNITHOLOGICAL LITERATURE		336
<p>Gordon H. Orians and Gene M. Christman, <i>A Comparative Study of the Behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds</i>, reviewed by Robert W. Nero; Merrill Wood, <i>A Bird-Banders Guide to Determination of Age and Sex of Selected Species</i>, reviewed by Robert C. Leberman; John K. Terres, <i>From Laurel Hill to Siler's Bog</i>, reviewed by Louise de Kiriline Lawrence; William Service, <i>Owl</i>, reviewed by Sally H. Spofford.</p>		
PUBLICATION NOTES AND NOTICES		314, 319
PROCEEDINGS OF THE FIFTY-FIRST ANNUAL MEETING	<i>Jeff Swinebroad, Secretary</i>	343

THE NESTING ECOLOGY AND REPRODUCTIVE PERFORMANCE OF THE EASTERN MEADOWLARK

JOHN L. ROSEBERRY AND W. D. KLIMSTRA

THIS paper reports on a study of 450 nests of the Eastern Meadowlark (*Sturnella magna*) near Carbondale, Illinois from 1960 to 1967. Data were collected in conjunction with long-term field studies of the Bobwhite (*Colinus virginianus*) conducted jointly by the Illinois Natural History Survey, Urbana and the Cooperative Wildlife Research Laboratory of Southern Illinois University.

Despite the abundance of meadowlarks, their wide-spread distribution, and membership in a relatively well-studied family (Icteridae), the nesting habits and breeding biology of the species have received surprisingly little attention. This probably reflects the difficulties involved in finding large numbers of these well-concealed nests. Nice's (1957) classic review of the nesting success of 17 open-nesting, altricial species contains no reference to meadowlarks; nor does Davis' (1955) list of studies on clutch size of 53 species of birds. Saunders (1932) gave breeding dates, nesting success, and clutch size of Eastern Meadowlarks near Ithaca, New York. Lanyon (1957) reported on nest success and clutch size of both Eastern Meadowlark and Western Meadowlark (*Sturnella neglecta*) near Madison, Wisconsin, and Johnston (1964) noted breeding season and clutch size of both species for Kansas. Sample sizes reflected by these studies ranged from 16 to 62 nests. Data presented by Gross (*in Bent*, 1958) represent largely the contribution of Saunders (1932). In addition to these studies, numerous accounts of a few nests are reported in the literature but the small sample size, lack of certain details, and variation in observational and reporting techniques make them of limited value.

STUDY AREAS AND METHODS

Studies were conducted primarily on the Carbondale Bobwhite Quail Research Area, a 1450-acre tract of privately-owned farms located 6 miles northeast of Carbondale in Jackson and Williamson Counties, Illinois. The topography is gently rolling and soils are of low productivity. Meadowlark nesting habitat is mainly represented by permanent pastures and hayfields which occupy some 27 per cent of the area; approximately 31 per cent of the acreage is planted yearly to corn and soybeans, 10 per cent is woods and 20 per cent is idle or fallow land. One 50.5-acre pasture (40 acres of nesting cover) on the west border of the Research Area, hereafter referred to as Bigler's pasture, served as a focal point for studies during the latter phase of the project. Some nests were also located on University-owned farmland just south and west of the main campus of Southern Illinois University in Jackson County.

Nest searching methods were identical to those employed in finding Bobwhite nests. Walking abreast, at intervals of 4 feet and with the aid of walking sticks, crews of four

to eight men systematically searched all cover. From 1960 to 1963, the entire Carbondale Research Area, excluding woodlots and intertilled cropland, was searched at least twice; in 1964, selected portions of this area were hunted and in 1965, one field on the Research Area (Bigler's pasture) and selected fields on the University property were hunted. In 1966 and 1967 a limited amount of nest hunting was conducted on the University property.

From 1960 to 1963, nest hunting was begun around 20 May and terminated 10 September; in 1964 hunting was conducted during the periods of 10-19 June and 13-25 August. In 1965, fields were searched from 10-19 May and 16-25 June. All fields searched were covered at least twice except during 1965, 1966, and 1967 when portions of the University properties were hunted only once.

When found, each nest was marked; active nests were revisited every 3-4 days until final outcome was established. When nests were no longer active, fate, approximate date of egg laying, number of eggs, plant materials in the nest, degree of overhead cover and concealment, direction of nest entrance and slope, and drainage at the nest site were recorded.

THE NEST

Construction.—Actual nest construction was not witnessed during the study; this activity has been described by Saunders (1932:178-180). He believed that only the female participated in nest building, which normally took from 3 to 5 days, even though numerous earlier workers had credited both sexes. Lanyon (1957) found that earlier nests took from 6 to 8 days to complete but later nests were built in as few as 4 days.

Nests were virtually always in a slight bowl-like depression. This bowl, normally from 1 to 3 inches deep and 4 to 4½ inches in diameter, was apparently scraped out by the bird prior to nest construction but on occasion, deeper natural depressions such as hoofprints of cattle or horses were used. As described in detail by Saunders (1932:180-181), a typical meadowlark nest consists of (1) an inner subspherical shell composed of a shallow bowl of finely woven grass stems on which the eggs are laid and a thin subspherical superstructure of coarser stems placed between the shell and the ground and (2) an outer covering of coarse grass or other material bent over the shell to form a canopy.

Most nests found during our study conformed to the above type, however, there were numerous exceptions. Form and degree of construction seemed at least partially dependent upon time of nesting season and type of cover in the immediate area. Some nests were large structures with thick sides and heavy, complete roofs closely resembling those of the Bobwhite while others lacked both sides and top, consisting only of the inner subspherical shell of fine stems with some coarser plant material beneath it. The most common nest type was intermediate between these extremes; it consisted of a complete subspherical structure, often tilted at a 20° to 30° angle with the back of the nest built up to form a partial canopy. Of 220 used nests, 17.3 per cent lacked a canopy;

44.5 per cent had a partial canopy; and 38.2 per cent had a full canopy. Occasionally, nests were located so as to use the natural canopy provided by lodged grasses.

The time of nesting clearly influenced nest architecture. Of those nests built prior to 26 May, 21.0 per cent lacked a canopy, 53.2 per cent had a partial canopy, and 25.8 per cent had a full canopy. Of those built after 26 May, only 12.1 per cent lacked a roof, 36.4 per cent had a partial roof, and 51.5 per cent had a full canopy. This increase in the construction of elaborate nests possibly reflected seasonal enrichment of the vegetation. Interestingly, Lanyon (1957) found that early nests generally took from 2 to 4 days longer to complete than later nests yet our data showed the former to be generally less elaborate than the latter.

Several writers (Gross *in* Bent, 1958; Saunders, 1932; Lanyon, 1957; and Thoms, 1924) reported nests with obvious trails, and even covered passageways or tunnels, leading to them through the vegetation. The presence of such covered passageways was not observed during our study although in a few instances, rather obvious runways were noted leading to the entrance of the nest.

Building materials.—As noted by Saunders (1932) and circumstantially confirmed during our study, the female tended not to use plants present at the nest site for the inner lining of the nest but almost always brought this material from a considerable distance. On our study areas, the material most commonly used for the inner subspherical shell was the fine-stemmed, grass-like rush *Juncus tenuis*. This plant was seldom found growing at the nest site. Of 853 plant occurrences in 406 nests, grasses and grass-like forms (*Juncus* and fine-stemmed legumes) accounted for 823 or 96.5 per cent (Table 1). In all, 32 individual plant species were identified in 406 nests. *Juncus*, whose use was limited almost exclusively to the inner lining, occurred in 63.3 per cent of the nests. Fine stems of bluegrass or lespedeza were most often used as substitutes for *Juncus* in the nest lining. Meadow fescue at times was found in the canopy but mainly was used in the subspherical superstructure. When fescue was not available, other coarse-stemmed species such as timothy, orchard grass, wheat, and rye were used. Of the nests examined, 81.6 per cent were constructed of more than one species of plant with 56.7 per cent containing two and 21.4 per cent containing three; five different species were the most found in any one nest.

Concealment and drainage.—Nests were rated on the basis of concealment to the human eye, a factor influenced by the amount and type of vegetation in which the nest was situated and to a lesser extent the presence or absence of a nest canopy. Of 377 nests, 19.1 per cent were judged to have excellent concealment. These were difficult to see even when the location was known within

TABLE 1
PLANT MATERIALS USED IN THE CONSTRUCTION OF 406 MEADOWLARK NESTS

Species	Frequency of occurrence	
	Number	Per cent
Rush (<i>Juncus</i> spp., mostly <i>tenuis</i>)	257	63.3
Cheat (<i>Bromus secalinus</i>)	168	41.4
Meadow fescue (<i>Festuca elatior</i>)	95	23.4
Bluegrass (<i>Poa compressa</i> and <i>pratensis</i>)	77	19.0
Common and Korean lespedeza (<i>Lespedeza striata</i> and <i>stipulacea</i>)	46	11.3
Panic grasses (<i>Panicum</i> spp.)	30	7.4
Common tickle grass (<i>Agrostis hyemalis</i>)	27	6.7
Small wild barley (<i>Hordeum pusillum</i>)	24	5.9
Paspalums (<i>Paspalum</i> spp.)	18	4.4
Red clover (<i>Trifolium pratense</i>)	17	4.2
Timothy (<i>Phleum pratense</i>)	15	3.7
Orchard grass (<i>Dactylis glomerata</i>)	14	3.4
Foxtail grasses (<i>Setaria</i> spp.)	10	2.5
Crabgrasses (<i>Digitaria</i> spp.)	9	2.2
Wheat (<i>Triticum aestivum</i>)	8	2.0
Slender fescue (<i>Festuca octoflora</i>)	6	1.5
Corn (<i>Zea mays</i>)	4	1.0
Broomsedge (<i>Andropogon virginicus</i>)	4	1.0
Lance-leaved ragweed (<i>Ambrosia bidentata</i>)	4	1.0
Redtop (<i>Agrostis alba</i>)	4	1.0
Plantains (<i>Plantago</i> spp.)	3	0.7
Low hop-clover (<i>Trifolium procumbens</i>)	3	0.7
Oak (leaves) (<i>Quercus</i> spp.)	2	0.5
Rye (<i>Secale cereale</i>)	2	0.5
Yarrow (<i>Achillea millefolium</i>)	1	0.2
Alsike clover (<i>Trifolium hybridum</i>)	1	0.2
Elm (leaves) (<i>Ulmus</i> sp.)	1	0.2
Sedge (<i>Carex</i> sp.)	1	0.2
Rough buttonweed (<i>Diodia teres</i>)	1	0.2
Dropseed (<i>Sporobolus</i> sp.)	1	0.2

a square yard or so; often, they became visible only after the vegetation was parted directly over them. A rating of good was given to 47.8 per cent of the nests; these were visible from above without intense searching. Ratings of fair and poor were given to 28.9 per cent and 4.2 per cent, respectively; the latter classification applied to nests visible from several yards away. Nice (1964) found a positive correlation between nest success of the Song Sparrow (*Melospiza melodia*) and degree of nest concealment; but, no such relationship was evident from our data.

TABLE 2
ORIENTATION OF MEADOWLARK NESTS IN SOUTH-CENTRAL WISCONSIN
AND SOUTHERN ILLINOIS

Direction Nest Facing	Wisconsin ¹		Illinois ²	
	Number	Per cent	Number	Per cent
North	19	14.5	49	14.0
Northeast	23	17.6	74	21.2
East	36	27.5	48	13.7
Southeast	13	9.9	39	11.1
South	11	8.4	33	9.5
Southwest	5	3.8	39	11.1
West	5	3.8	29	8.3
Northwest	19	14.5	39	11.1
Totals	131	100.0	350	100.0

¹ Calculated from Lanyon (1957, Table 8, p. 42).

² Our study.

When nesting in areas of gently rolling or moderately hilly terrain, meadowlarks showed a definite affinity to slopes as opposed to flat crests or valleys. Of 412 nest sites, drainage was considered excellent for 37.1 per cent and good for 45.2 per cent. These represented nests which would not be expected to flood or wash out except possibly under torrential conditions. Only 12.4 per cent and 5.3 per cent of the nest sites were classified as having fair or poor drainage, respectively. The latter type included nests which could be flooded by surface runoff during moderate to heavy rain showers.

Orientation.—Earlier workers have noted that orientation of meadowlark nests appears to be non-random. In northern Illinois, Sandborn and Goelitz (1915) found eight nests of *S. magna*, all of which had entrances facing south. Saunders (1932), from observations of 29 *S. magna* nests in New York, concluded that orientation might be in any direction but suggested a possible correlation with the location of male song perches. Lanyon (1957:42), reporting on 131 nests of *S. magna* and *S. neglecta* in Wisconsin, found nests to face predominantly to the north and east. He found no relationship with position of the nest within the territory or with location of male song perches but stated: "The effect of the prevailing winds, particularly during rain or sleet storms, is to depress the vegetation toward the north and east, thus encouraging the same orientation in nidification."

As shown in Table 2, Lanyon's (1957) data showed 59.6 per cent of 131 nests faced north, northeast, or east with east the modal direction. In our study, 48.9 per cent of 350 nests faced in one of these three directions with

northeast being the modal direction; a chi square test showed this orientation pattern not to be due to chance ($P < 0.001$). Interestingly, 48.7 per cent of 915 Bobwhite nests located over a 15-year period in the same general area also faced either north, northeast, or east (Klimstra, unpublished data). Seemingly then, the factor or factors responsible for this non-random orientation similarly affect both the Bobwhite and the meadowlark. As in Wisconsin (Lanyon, 1957), nests on our study areas also tended to face away from prevailing winds. Records (unpublished data, Murdale Airport, Carbondale) from 1954 through 1963 indicated that during the period of 1 April through 21 July, winds blew toward the north and north-northeast 33 per cent of the time and field observations confirmed that vegetation, especially grasses, tended to be lodged in those directions.

Nest orientation also seemed related to the direction of slope upon which the nest was located. Hann (1937) noted that 31 of 36 (86 per cent) Ovenbird (*Seiurus aurocapillus*) nests faced down the slope at some angle although he found no affinity for any one particular direction. In our study, 47.6 per cent of the nests faced down slope at some angle while only 29.8 per cent faced up the slope ($P < 0.001$). This tendency to face nests down slopes does not entirely explain the non-random orientation as 44.7 per cent of those nests built on slopes other than north, northeast, or east faced in one of these three directions ($P < 0.05$).

Unused nests.—Saunders (1932) observed that females commonly began and worked on several nests before one site was completed. In our study, 126 of 388 (32.5 per cent) nests were thought not to have been used. Some of these were only partially built but others were indistinguishable from active nests with respect to construction. Regarding degree of construction, 32.0 per cent of the unused nests had no canopy and only 18.0 per cent had full canopies as compared to 17.3 per cent and 38.2 per cent, respectively, for used nests.

Saunders (1932) believed that the partial building of several nests occurs just prior to the female attaining the sexual and physiological stage necessary for intensive nest building. Our data tend to support this in that unused nests were much more common during early stages of the breeding season. While in most instances it was impossible to determine the date of commencement of these unused nests, for those in which dating was possible, virtually all were begun before 12 May.

THE BREEDING SEASON

The beginning and duration of a species' nesting season are important to overall reproductive performance. They determine the climatic conditions, or range of conditions, the young must cope with, and whether sufficient time is

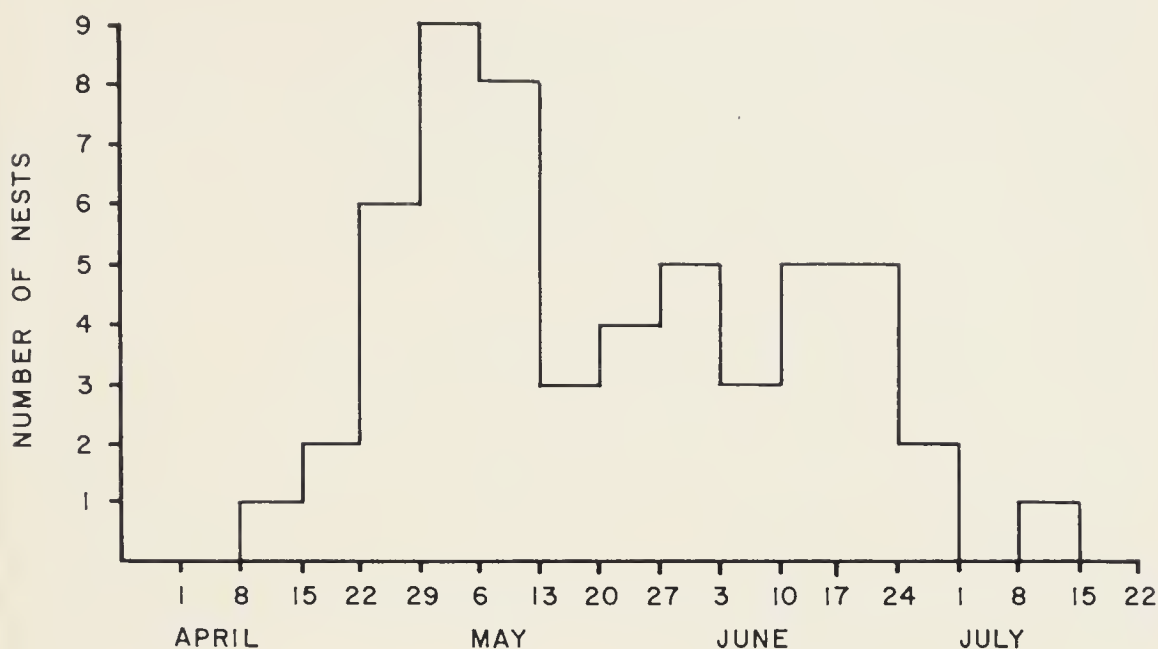


FIG. 1. Initial egg laying dates for 54 Eastern Meadowlark nests, 1965.

available to the adults for raising more than one brood or renesting after nest failure.

Our study did not attempt to correlate beginning of nesting with environmental factors, and, as the start of nest hunting efforts was not uniform from year to year, we were unable to determine whether yearly variations in nesting time occurred. It has been established that meadowlarks breed later in the northern parts of their range (Saunders, 1932; Gross *in* Bent, 1958; Lanyon, 1957; Johnston, 1964). At approximately 38° latitude (southern Illinois, Kansas, Virginia), meadowlarks apparently begin laying around 10–15 April, end around 15–22 July, with peak activity from 29 April–5 May. At 42 – 43° latitude (Massachusetts, New York, Wisconsin) earliest laying is from about 23 April–5 May, latest from 4–15 July, with heaviest laying around 13 May.

Our study provided estimated dates of initial egg laying for 129 nests. Dates were calculated by backdating from the particular event (laying, incubating, brooding) in progress when the nest was discovered. Unfortunately, nest searching efforts during the first four years of the study were begun in late May or early June; consequently, many of the nests found were too old to permit estimation of egg-laying dates. Those nests which were dated (75) during these years cannot be used to analyze the entire nesting season as they mostly represent mid- to late-season efforts. In 1965, nest searching was begun in early May, and the 54 nests dated during that year were representative of the entire breeding season. The earliest recorded date of egg laying was 14 April with most eggs being laid during the period of 22 April to 12 May, the

modal period being from 29 April to 5 May (Fig. 1). Dates of initial egg laying recorded during 1960–1964, while not reflecting early nesting, can be combined with those from 1965 to analyze the latter portions of the breeding season. It is apparent that on our study areas, meadowlark nesting is virtually completed by 7 July as only 3 (2.3 per cent) of 129 nests were begun after this date. The latest recorded nest was begun on 23 July and hatched on 8 August 1962.

No obvious peak for second brood nests is evident (Fig. 1), yet we suspect that most second brood nests were not begun until the middle of May or later. Theoretically, if second brood nests were begun shortly after fledging of the first brood, a second nesting peak should have been evident about 30 days after the first peak. However, as over $\frac{2}{3}$ of all nests failed at varying times after their commencement, renesting following these failures would tend to be staggered in time, thus smoothing out the nesting curve by overlapping and obscuring second brood nesting peaks.

NESTING IN RELATION TO LAND-USE TYPES

All land-use types on the Carbondale Research Area except intertilled cropland and woods were searched for nests from 1960 through 1963; only selected fields were hunted during 1964–1967. Acreage figures used in the calculation of nest densities per land-use type (Table 3) were obtained by multiplying the acreage of each tract by the number of years it was searched. Data from random, non-systematic hunting, i.e. coverage not designed to find all nests in a particular area, were not included in these calculations. A total of 435 nest locations were recorded, however, only 307 nests that contained eggs will be considered here; there appeared to be no major differences in proportions of unused nests among the various types of nesting cover.

Saunders (1932) noted that while grasslands and pastures support larger meadowlark populations than other habitats, the birds commonly nest in a wide variety of cover-types. Data from our study indicates that the preferred nesting habitat is pasture, followed in order by hayfields, soilbank fields, winter wheat fields, idle, and fallow areas (Table 3). In all these areas, however, the presence of dead grass stems at ground level and the absence of woody vegetation or numerous shrubs in the immediate vicinity appeared to be a prerequisite for nesting utilization. Height of cover at 204 nest sites ranged from 2 to 30 inches and averaged 14.9; 66.6 per cent of all nests were built in cover 10 to 20 inches high. The fact that nests are sometimes built in rather deep bowls or natural depressions often permitted utilization of areas with little cover: one nest was found in the mowed fairway of a golf course.

Pastures.—Condition and composition of pastureland on the study area

TABLE 3
MEADOWLARK NEST DENSITY IN RELATION TO LAND-USE TYPES

Land-use type	Acreage searched for nests	Nests found ¹	Nests per 100 acres
Pasture			
grazed	879	120	13.7
ungrazed ²	80	80	100.0
Total	959	200	20.9
Hayfield			
alfalfa	120	5	4.2
red clover	222	35	15.8
mixed grasses ³	62	11	17.7
Total	404	51	12.6
Soilbank (grasses)	487	25	5.1
Winter wheat ⁴	83	4	4.8
Idle	558	21	3.8
Fallow	298	6	2.0
Totals	2,789	307	11.0

¹ Used nests only.

² First and second year subsequent to removal of cattle.

³ Predominantly meadow fescue, orchard grass, timothy, bluegrass, and cheat.

⁴ Two built prior to cutting of wheat, two built in wheat stubble.

varied greatly. There was opportunity to compare utilization among lightly grazed to severely overgrazed pastures and one field left ungrazed for 2 years. Also compared were pastures receiving similar grazing pressure but composed of entirely different floral communities.

In all, 200 nests were found on 959 acres of pasture (20.9 nests per 100 acres). This, the heaviest utilization of any land-use type, mainly reflected the extremely high number of nests (80) found on one 40-acre pasture during 2 years that it was ungrazed. Nesting utilization of grazed pastures (13.7 per 100 acres) was only slightly greater than hayfields (Table 3).

We found an inverse relationship between intensity of grazing and utilization by nesting meadowlarks. An example is offered by one 40-acre field containing approximately 60 per cent meadow fescue, 35 per cent Korean lespedeza, 5 per cent orchard grass, and no herbs and shrubs. During 1961, 1962, and 1963, the heavy grazing of this field by cattle maintained the vegetation at a height of about 1 to 3 inches and left only a few scattered clumps of fescue 12 or more inches in height. During these years, three, two, and three nests with eggs, respectively, were found. In 1964, grazing was less intense, resulting in a more abundant and uniform distribution of fescue clumps

and leaving patches of Korean lespedeza up to 5 inches in height. Eleven nests with eggs (19 including unused nests) were found that year, nearly all of which had been built in patches of lespedeza or at the base of isolated clumps of fescue. The most striking example of the effects of grazing on nest establishment was evident in Bigler's pasture. Herbaceous vegetation in this field consisted mainly of meadow fescue, cheat, lance-leaved ragweed, Korean and common lespedezas, and panic grasses; many other species were also represented. During 1960, the field was heavily grazed and three nests were found; in 1961 it was severely overgrazed and no nests were found. In 1962, grazing was heavy but less than the previous years and 13 nests were built in the field. In the spring of 1963, the pasture was renovated, manure spread, and Kentucky bluegrass seeded on about $\frac{2}{3}$ of the field and meadow fescue on $\frac{1}{3}$; 12 nests were found that season. In 1964 and 1965, the field was not grazed and exhibited large areas of dead and lodged stems of bluegrass and vigorous stands of fescue. During these years, 41 and 39 nests with eggs, respectively, were found. Considering both used and unused nests, this field yielded a total of 129 nests in 2 years, a far higher density than was recorded on any other plot during the entire study.

Hayfields.—As shown in Table 3, hayfields ranked second to pastures as favored nesting sites with an average density of 12.6 nests per 100 acres. Alfalfa (*Medicago sativa*) fields were least preferred (4.2 per 100 acres): red clover fields yielded 15.8 nests per 100 acres. Nesting was heaviest in a mixed-grass hayfield (mainly orchard grass, meadow fescue, timothy, bluegrass, and cheat) which averaged 17.7 nests per 100 acres over a 2-year period.

Alfalfa fields, especially good stands, seemingly lacked sufficient grassy cover at ground level to provide acceptable nesting habitat. This was also apparent in most red clover fields, but portions of these fields were sparse enough to allow the invasion of grasses thus providing some nesting cover. Red clover appeared in 17 nests (Table 1); it was, however, always used in conjunction with other, more finely-stemmed species. Alfalfa stems were not found in any nest.

Soilbank and wheat fields.—In 1959, five fields on the Research Area totalling 155 acres were placed in the Federal Soil Bank Program; this acreage was reduced to 135 by 1961. Under provisions of this program, fields were taken out of cultivation and seeded to grasses; mowing was permitted but fields could not be pastured or used for hay. Meadowlark utilization of these areas was not great; overall density averaged 5.1 nests per 100 acres. Once established, four of the plots displayed dense, uniform stands of meadow fescue with some orchard grass and Korean lespedeza; few nesting birds used them. The remaining field, 33 acres of gently sloping land, apparently re-

ceived a poor initial seeding and remained rather weedy throughout the period of study. During the last 2 years fescue, while retaining good stands in the lower moist areas, virtually disappeared from the dryer slopes and ridges and was replaced by a variety of invading species, especially common lespedeza, panic grasses, and rough buttonweed. During these two years, this field comprised only 13.5 per cent of the total soilbank acreage searched but yielded 40.0 per cent of the nests found.

Wheat fields, showing a density of 4.8 nests per 100 acres, seemingly did not provide good nesting habitat; this probably reflected a general lack of grasses and fine-stemmed legumes necessary for nest construction. Two of four nests in wheat were built after fields had been harvested.

Idle and fallow areas.—Although 558 acres of idle and 298 acres of fallow land (uncultivated for 1 or 2 years) were searched during the study, only 27 used nests were discovered in these habitats (Table 3). This represents a nest density of 3.8 and 2.0 per 100 acres, respectively, the lowest encountered in all types of cover.

Fallow fields were thought to be little used because of an absence of sufficient grassy cover. In this region, most areas left uncultivated are initially invaded by such species as common and Korean lespedeza, plantains (*Plantago* spp.), wild lettuce (*Lactuca* spp.), lance-leaved ragweed, cocklebur (*Xanthium* spp.), and foxtails (*Setaria* spp.). Cheat, panic grasses, and crabgrass are early invading grasses, but the amount of dead stems suitable for good nesting material is generally lacking during the year or two subsequent to fallowing.

Most idle areas searched were at least 6 years or older and were characterized by numerous woody shrubs, small trees, and patches of briar (*Rubus* spp.), intermixed with a variety of herbaceous plants and such grasses as cheat, broomsedge, and bluegrass. In many instances, the ground cover with growing grasses and dead and lodged stems looked ideal for nesting cover; however, the presence of numerous herbs and small woody species apparently precluded extensive use by meadowlarks. Those areas which received moderate use were recently idle fields which contained little or no woody cover, yet provided a better ground cover of grasses than did fallowed areas.

CLUTCH-SIZE

As pointed out by Davis (1955), published clutch-size data usually refer to the number of eggs found in nests presumed to contain complete clutches. In practice, the investigator can rarely be certain that the eggs present represent a complete clutch, i.e. the number of eggs laid in an uninterrupted series. In our study, egg counts of presumably complete clutches were available from 101 nests. Included in this sample were nests discovered while eggs were be-

TABLE 4
SEASONAL VARIATION IN THE CLUTCH-SIZE OF MEADOWLARKS

Date first egg laid	Number of eggs					Mean	Standard Deviation
	2	3	4	5	6		
14 April-5 May	0	1	1	6	1	4.78	0.79
6 May-2 June	0	5	11	18	0	4.38	0.74
3 June-30 June	2	12	26	13	0	3.94	0.80
1 July-23 July	0	3	0	2	0	3.80	0.98
Totals	2	21	38	39	1	4.16	0.83

ing deposited and subsequently observed to be incubated, and nests discovered during incubation. Conceivably, this latter group could have included some nests from which one or more eggs had been removed prior to incubation; however, observations from this study and those from a study of over 1,000 Bobwhite nests (Klimstra, unpublished data) clearly suggest that in virtually all instances of nest disturbance by predators, enough eggs (usually all) are affected to make the disturbance easily detectable. Nests found subsequent to destruction or abandonment were excluded from clutch-size calculations, as were nests containing young because of the possibility that unhatched eggs had been removed from the nest by parent birds.

The mean number of eggs found in 101 complete clutches was 4.16 ± 0.08 . Clutches varied from two to six (Table 4). As explained previously, our sample contained a disproportionately large number of mid- and late-season nests, and, as shown in Table 4, clutch-size tended to decrease as the nesting season progressed. Thus, it seems justified to assume that the mean clutch-size derived may be somewhat low. During 1965, approximately 60 per cent of all nests were started prior to 27 May and 40 per cent after that date: data from all years showed a mean clutch-size of 4.36 for the earlier period and 4.03 for the latter. Using these figures, a prorated mean clutch-size of 4.23 is obtained.

The average number of eggs per nests in our study proved considerably lower than previously reported for the Eastern Meadowlark. Lanyon (1957), from 38 nests in Wisconsin, reported a mean clutch-size of 4.81 ± 0.16 with a range of 2-6. From Saunders' (1932:197) New York data, a mean clutch-size of 4.57 ± 0.15 was calculated for 23 nests. Gross (*in Bent*, 1958) stated that Eastern Meadowlark clutches vary from 3 to 7 with sets of 5 most common and sets of 4 more usual in second brood nests. He also noted that clutches tended to be smaller in the southern part of the nesting range while Saunders (1932) found that clutches in central Oklahoma averaged smaller

than those from New York. Our data, indicating smaller clutches than those reported from Wisconsin and New York, would seem to support this. Johnston (1964), however, found a mean of 5.2 eggs (range 4–7) for 26 nests in Kansas which is approximately the same latitude as southern Illinois.

Davis (1955) cited numerous studies demonstrating that clutch-size in most species of birds decreases as the nesting season progresses; renesting apparently produces fewer eggs than initial nesting. Such seasonal decline in size of meadowlark clutches has been noted also by Johnston (1964), Saunders (1932), Gross (*in* Bent, 1958), and Lanyon (1957). The latter author found a seasonal decline in the size of Western Meadowlark clutches but data for the eastern species from the same area failed to demonstrate this. We were unable to differentiate among first and second brood nests and renesting efforts, but our data (Table 4) clearly show a seasonal decline in the number of eggs laid. Average clutch sizes recorded for the periods 14 April–5 May, 6 May–2 June, 3 June–30 June, and 1 July–23 July were 4.78, 4.38, 3.94, and 3.80, respectively.

Size of eggs.—According to Bendire (1895), 201 Eastern Meadowlark eggs in the United States National Museum averaged 27.75 mm by 20.35 mm. The largest egg was 30.78 by 22.61 mm while the smallest was 21.59 by 18.29 mm. Reed (1965) stated that egg size for this species was 27.94 by 20.32 mm but gave no range or sample size. From our study areas, mean length of 17 eggs from 9 nests was 27.97 ± 0.44 mm (range 23.54–30.62) and mean width was 20.69 ± 0.29 mm (range 18.40–23.76).

NESTING SUCCESS AND LOSSES

Determination of nest fate.—Lack (1954) believed the problems of accurately estimating nesting success have not always been appreciated. Mayfield (1960 and 1961) contended that the sampling procedure used in some past nesting studies resulted in overestimating the percentage of successful nests and eggs. Nolan (1963:306) summarized Mayfield's argument:

“Briefly, the error consisted of calculating success from the fates of all nests found while still in use, regardless of the fact that, in many, development had already advanced into the incubation or nestling stages when the nests were discovered. Nests that had failed before they were found were usually disregarded. Such calculations thus overlooked both the success already attained by some nests (and the commensurately reduced risks ahead) and the losses already incurred by other nests. This kind of sampling . . . tended toward bias by selecting nests already partly successful and then measuring success during that subsequent fraction of their histories in which they were under scrutiny by the investigator. . . .

“To avoid this error, a study of observed nest success could be based on nests found at or before the moment the first egg is laid. (Alternatively, it would be theoretically possible for the observer to rely on nests found at any stage of development either if his

coverage of his study area were efficient enough to lead to the discovery of all nests while they were still in use by the birds, or if he could find, recognize, and include in his computations nests that had already failed.)”

Our calculations of nesting success are based upon the assumption that Nolan's second contingency was satisfied, that is, all nests, regardless of whether active or terminated, were found (or had equal chance of being found) and recognized.

Determination of the fate of nests no longer in use did present certain problems. It is extremely unlikely that an investigator can actually witness the culmination of the nesting process, even if the nest is kept under observation throughout the active period. Thus, determination of fate must be based generally upon evidence at the nest site. The accuracy of this is contingent not only upon the quality and quantity of the evidence but also upon the investigator's ability to correctly interpret it. Experience gained from the study of hundreds of Bobwhite nests greatly increased our ability to read “sign” at the nest site. However, because hatched meadowlark nests contain no egg fragments and because the eggs are much more fragile (apparently because they lack a strong shell membrane), the evidence at meadowlark nest sites was generally less and of poorer quality than at Bobwhite nests. Careful examination of nests known to have contained young which had fledged provided an index to the usual appearance of nests at this stage. While young are in the nest, emergence of the primary wing feathers produces an abundance of flaky, whitish material (feather sheaths) which collects in the bottom of the nest, ultimately sifting down through the lining to the bottom of the nest bowl. This was the primary criterion used to determine if a nest had contained young. Also the interiors of nests that had contained young were generally enlarged. It is possible that predation on young could have gone undetected if the young were removed either prior or subsequent to emergence of their primaries; however, evidence from several nests indicated that removal of young by predators left signs that could be interpreted.

Nests found without eggs or fragments and showing no sign of the presence of young or previous use were classified as unused. It is possible that some nests in which eggs were removed by snakes were erroneously placed in this category; however, nest interiors in which females had laid and incubated eggs were thought distinguishable in most cases from those which had never been used. Determination of specific predators was difficult because meadowlark eggs are extremely fragile and tend to break into tiny fragments once destroyed. While making identification of specific predators difficult, this virtually assured that some egg fragments would remain in a nest destroyed by a carnivore. Nests considered destroyed by predators could, of course, have

TABLE 5
PRODUCTIVITY OF MEADOWLARK NESTING ON STUDY AREAS, SOUTHERN ILLINOIS

	Bigler's pasture	All other areas	Total
Total nests found	170	280	450
Nests of unknown fate	13	49	62
Unused nests	60	66	126
Active nests of known fate	97	165	262
Per cent hatched	23.7 (23)	45.5 (75)	37.4 (98)
Per cent fledged	17.5 (17)	38.2 (63)	30.5 (80)
Total eggs examined 577			
Per cent hatched 42.1 (243)			
Per cent fledged 33.8 (195)			

already been abandoned before destruction; but, as will be shown later, this probably occurred very infrequently.

Of 450 meadowlark nests found, the fate of 62 could not be determined and 126 were unused; these were not included in computations of productivity. Analysis of nesting success, then, was based upon observations of 262 nests of known fate. The fate of individual eggs and nestlings were based upon observations of only a portion (170) of all nests; these represented nests in which the number of eggs laid, and their ultimate fate were known with reasonable certainty.

Success of nests, eggs, and young.—Of 262 active nests, the eggs of 98 (37.4 per cent) hatched and the young of 80 (30.5 per cent) fledged (Table 5): a "hatched nest," as used here, refers to one in which at least one egg hatched and a "fledged nest" is one from which at least one nestling successfully left the nest. Hatching and fledging success of 577 eggs was 42.1 per cent and 33.8 per cent, respectively. These data indicate a somewhat lower success than previously recorded for meadowlarks and other open-nesting, altricial species. Lanyon (1957) reported a total fledging success of 34.4 per cent for 60 *S. magna* and 62 *S. neglecta* nests in Wisconsin. In a review of 35 studies of open-nesting, altricial birds (not including meadowlarks), Nice (1957) found an overall fledging success of 49.3 per cent for 7,788 nests; hatching success of 21,040 eggs was 59.8 per cent while fledging success of 21,951 eggs was 45.9 per cent.

Overall productivity (Table 5) was lowered considerably by the extremely high losses incurred on one field of the study area (Bigler's pasture). Here, only 17.5 per cent of 97 nests fledged young as compared to 38.2 per cent of

165 nests on all other portions of the study areas. Factors thought responsible for this differential success will be discussed later.

A comparison of success of nests found before and after termination is of interest in light of Mayfield's comments previously cited (Nolan, 1963:306). This comparison is useful also in determining the possible effects of human visitations to the nest. The percentages of abandoned and preyed upon nests were 2.2 per cent and 3.4 per cent lower, respectively, in nests found while active as compared to those found after termination; this strongly suggests that careful visitations to the nest did not increase the incidence of abandonment or predation. On the other hand, fledging success was 21.3 per cent higher in nests found while active. This seems mainly to reflect the fact that hayfields were hunted after mowing, thus that portion of the nest sample found after termination includes almost all the nests destroyed by mowing.

Comparative losses of nests, eggs, and young.—Nesting efforts of birds are usually described in terms of percentage of successful nests, percentage of successful eggs, or both. Nolan (1963) noted that when only nest success is calculated, a nest which hatched only one egg received the same credit as a nest in which the entire clutch hatched. He felt that while this test was a fair indicator of predation, which normally results in all eggs being lost, it gave no measure of partial failure due to infertile eggs or embryonic mortality. Kalmbach (1939:592) stated: "Estimations on the basis of eggs hatched will regularly tend to disclose a lower degree of success than that based on so-called successful nests." Nice (1957) found that for 18 studies she reviewed, the percentage of eggs which produced fledgling young was lower than the percentage of nests which produced at least one fledgling young; but, she noted that egg success could be higher if many nests containing incomplete clutches were deserted (or destroyed) and if all eggs hatched in most successful nests.

Our findings, contrary to the above, revealed that the percentage of successful eggs was higher than nests. This mainly reflected the low number of unhatched eggs in successful nests and the large number of incomplete clutches destroyed by predators.

Our data showed a significantly higher survival rate among nestlings than eggs; 42.1 per cent of all eggs laid were hatched while 80.3 per cent of all young hatched were fledged. Apparently, this is the normal situation in open-nesting, altricial birds; examination of 26 studies (Nice, 1957:306-307) showed survival to be higher among young than eggs in 20 cases, lower in 5, and the same in 1. Using 18.5 days as the average length of time eggs occupy the nest (including laying) and 11.5 days as the average period young are in the nest, total losses of eggs averaged 3.1 per cent per day while losses of young aver-

TABLE 6
CAUSES OF NEST, EGG, AND NESTLING LOSSES FOR MEADOWLARKS, SOUTHERN ILLINOIS

Factor	Nests			Eggs ¹		Young ¹			
	No.	Per cent of lost nests	Per cent of all nests	No.	Per cent of lost eggs	Per cent of all eggs	No.	Per cent of lost young	Per cent of all young
Human disturbance	3	1.7	1.1	6	1.8	1.0	0	0.0	0.0
Abandoned	11	6.0	4.2	13	3.9	2.3	0	0.0	0.0
Destroyed by									
livestock	2	1.1	0.8	4	1.2	0.7	0	0.0	0.0
Destroyed by mowing	32	17.6	12.2	64	19.1	11.1	0	0.0	0.0
Predation	134 ²	73.6	51.2	226	67.7	39.2	46	95.8	18.9
Infertile eggs	—	—	—	7	2.1	1.2	—	—	—
Embryo mortality	—	—	—	4	1.2	0.7	—	—	—
Disappeared ³	—	—	—	10	3.0	1.7	2	4.2	0.8
Totals	182	100.0	69.5	334	100.0	57.9	48	100.0	19.7

¹ Based on observation of 170 nests.

² Eighteen of these were destroyed after hatching but prior to fledging.

³ No obvious sign of disturbance and nest not completely emptied.

aged 1.7 per cent per day. These average daily losses are not comparable to Nice's figures (1964) for the Song Sparrow, for she calculated the percentage of young lost by dividing the number lost by the number of eggs laid instead of dividing (as we did) the former number by the number of eggs hatched.

Several reasons for the higher survival of nestlings on our study areas are readily apparent. Infertility and embryonic mortality naturally affect only eggs, and desertion by the female occurs much more frequently (if not exclusively) before the eggs have hatched. Losses to mowing were rather high among eggs but did not affect young, although this must surely have been a matter of chance and timing as nests in all stages would be equally susceptible to this type of destruction. Losses to predators were more equal among eggs (2.1 per cent per day) and young (1.6 per cent per day) but still 1.3 times greater for the former if the relative time each was exposed to this hazard is taken into account. It is possible that nests containing eggs are more readily found by predators (eggs are somewhat more easily seen by humans than are the young), but we have no data to substantiate this. Rather, it is probable that those nests which are most vulnerable to predation (poorly concealed or located near hunting trails) would be found and destroyed sometime during the first 18 or so days before the eggs have hatched. Conversely, if nests survive this period without being preyed upon, it probably reflects optimum cover and concealment, hence a greater likelihood of remaining undetected throughout the remainder of their use.

Causes of Nest Failures

Abandonment.—Of 262 nests with eggs, 14 were abandoned by the female; a total representing 5.3 per cent of all nests and 7.7 per cent of all nest failures (Table 6). Saunders (1932) found that, occasionally, females deserted their nestlings; this was not observed in our study as all desertions occurred before the eggs hatched. Three nests were abandoned after having been slightly damaged by research workers; to our knowledge no other desertions were caused by human interference. Incubating females readily flushed from the nest upon approach but usually flew only a few feet off the ground and alighted within 20–30 yards of the nest. Some females were flushed as many as four times during the nesting cycle without causing desertion. At one extremely open nest site (in a mowed field) the senior author observed a female flush off the nest, fly a short distance, then land and run along the ground using the broken wing ruse. Almost immediately a male, which had been perched in a small shrub about 12 yards from the nest, alighted and began running from the nest at a 30° angle from the retreating female's path. He did not feign injury but moved slowly and stayed just ahead of the observer.

In addition to the three nest abandonments caused by human interference, 11 instances of abandonment from other causes were recorded during the study; at least two and possibly more of these were evidently due to parasitism by the Brown-headed Cowbird (*Molothrus ater*). Two nests each containing two eggs thought to be those of the cowbird were found; in one, a meadowlark egg was lying undamaged just outside the nest entrance. None of these cowbird eggs hatched, having apparently not been incubated. Of the remaining nine abandoned nests, four had single eggs lying just outside the nest, three contained a single egg in the nest, one had two eggs in the nest, and one had three eggs in the nest and one outside the entrance.

Friedmann (1963) and Gross (*in Bent*, 1958) believed the Eastern Meadowlark to be an uncommon host of the Brown-headed Cowbird. Saunders (1932) in a study of over 50 nests from New York and Oklahoma found no evidence of cowbird parasitism and Terrill (1961) reported only 1 of 52 nests parasitized in southern Quebec. Other workers, however, have noted more extensive use of meadowlark nests by cowbirds. In Wisconsin, Lanyon (1957) found cowbird eggs in 9 of 41 (22 per cent) *S. neglecta* nests and 6 of 38 (16 per cent) *S. magna* nests. In Nebraska, Hergenrader (1962) reported 5 of 31 (16 per cent) *S. magna* nests parasitized. Eifrig (1915 and 1919) wrote that he "repeatedly" found meadowlark nests containing cowbird eggs in the Chicago region.

Bobwhite eggs have also been found in meadowlark nests (Lackey, 1913); however, this apparently is uncommon and does not constitute nest parasitism

(Gross *in* Bent, 1958). On 29 May 1967, a female meadowlark was flushed from a nest containing five meadowlark and three quail eggs. On 6 June, the nest contained one newly hatched meadowlark along with the remaining undisturbed eggs; on 7 June, two meadowlarks had hatched with the quail eggs still present. The nest was revisited on 13 June and while it showed no sign of damage, all young and eggs were gone; they were believed removed by a snake.

Mowing and livestock.—Gross (*in* Bent, 1958:75) wrote: “. . . it is probably safe to state that more meadowlarks [nests] are destroyed by this means [mowing] . . . than by any other.” Losses inflicted by mowing operations during our study were relatively high but did not constitute the major source of nest destruction. Thirty-two nests were destroyed in this manner, a total representing 12.2 per cent of all nests and 17.6 per cent of all nest losses (Table 6). Twenty-two of these resulted from hay cutting, 7 from pasture mowing, 1 from wheat combining, and 2 from miscellaneous mowing. Only one female was killed at the nest by a mower. Probably the tendency of birds to readily flush upon approach accounts for this low figure.

Although 120 nests were located in areas grazed by livestock, only 2 were destroyed by trampling. During a 3-year period, Lanyon (1957) found 122 nests on 100 acres of permanent pasture on which 40–50 head of cattle grazed. He reported a loss due to cattle of 15 nests or 12.3 per cent of all nests and 18.8 per cent of all nest losses.

Predation.—Losses attributed to predation during our study amounted to 51.2 per cent of the nests (73.6 per cent of nest failures) and 47.1 per cent of the eggs and young (67.7 per cent of all egg losses and 95.8 per cent of all nestling losses). This is somewhat higher than the relative and total predation reported by Lanyon (1957) in Wisconsin; he found that 36.1 per cent of all nests were preyed upon and 55.0 per cent of all nest losses were due to predation.

Because they are always located at ground level, meadowlark nests are subject to predation by a variety of animals. Gross (*in* Bent, 1958) thought that domestic dogs and cats were especially destructive to nests located in fields adjacent to farm houses. Lanyon (1957) attributed most of the predation observed on his Wisconsin study area to the red fox (*Vulpes vulpes*) and domestic dog and cat, with skunks (*Mephitis mephitis*), thirteen-lined ground squirrels (*Citellus tridecemlineatus*), and garter snakes (*Thamnophis sirtalis*) also contributing. Saunders (1932) felt that the house cat was the most serious predator although weasels (*Mustela erminea*), skunks, and dogs also preyed upon nests. He suspected meadow mice (*Microtus pennsylvanicus*) and Common Crows (*Corvus brachyrhynchos*) as occasional destroyers of eggs.

The difficulty of assigning responsibility of individual nest destruction to specific predators has already been discussed. Of the 134 instances of predation on our study area, the precise predator involved was unknown in 100 cases. Of the remaining 34, 13 were attributed to snakes, 9 to house cats, 6 to skunks, 5 to foxes or dogs, and 1 to an avian predator. These data are misleading, however, for they imply that snakes were the most serious predators, when in fact, most of the 100 unknowns were mammals of one species or another.

As previously noted, the survival rate of nests and eggs was quite low on Bigler's pasture. Here, losses to predators amounted to 72.2 per cent of all nests and 87.5 per cent of all nest failures, as compared to 38.8 per cent and 62.7 per cent, respectively, for the remainder of the area. Similarly, nesting Bobwhite also suffered unusually heavy losses in this field during the same period (Klimstra, unpublished data). From 1954 through 1965, Bobwhite nest losses to predation amounted to 35.2 per cent on all areas other than Bigler's pasture. From 1954 through 1963, on Bigler's, Bobwhite suffered a 41.8 per cent loss to predators, but during the 2 years (1964 and 1965) when the field was not grazed and meadowlark nest density was highest, predators destroyed 24 of 29 quail nests (82.8 per cent) located in the field.

No detailed surveys were made of the kinds and numbers of predators present in this area. Nevertheless, routine observations in the course of nest hunting activities clearly indicated that this particular field served as hunting territory for an unusually large number of carnivores, especially during 1964 and 1965. Ten houses were located within $\frac{1}{4}$ mile of the field; five within 100 yards. At least six dogs were known to roam the field; house cats, while seen much less frequently, also hunted the area. While not thought overly abundant, red foxes, and possibly some gray foxes (*Urocyon cinereoargenteus*), were also present as evidenced by scat and sign. A 3.8-acre pond in the center of the field also attracted raccoons (*Procyon lotor*) and opossums (*Didelphis marsupialis*). Snakes were quite common; blue racers (*Coluber constrictor*) and prairie kingsnakes (*Lampropeltis caligaster*) were noted with regularity during the nest hunts. By far the most common carnivore, however, seemed to be the striped skunk. Numerous dens were located in and around a 4-acre woodlot near the center of the field while diggings and trails were numerous throughout the area. Frequently, skunks were seen in the field in daylight; as many as three different animals were observed in one morning.

In addition to predators, there appeared to be an extremely high population of prairie voles (*Microtus ochrogaster*). Runways and grass nests seemed uniformly abundant throughout the field and numerous voles were seen as we searched the ground for nests. It is our contention that instead of acting as

buffers, these rodents actually attracted predators to the area and held them for longer periods of time by making their hunting efforts more profitable. Because the finding of stationary and concealed nests is more or less a matter of chance, the percentage of these nests found must invariably increase in direct proportion to the number of "predator-hours" spent in the field. Stoddard (1931) also felt that high populations of rodents (cotton rats, *Sigmodon hispidus*) attracted predators which, once in the area, found and destroyed quail nests.

Infertile eggs and embryonic mortality.—Data concerning unhatched eggs in successful clutches were obtained from 63 nests which were under observation before and after hatching. Of 264 eggs in these nests, 7 (2.7 per cent) failed to hatch because of infertility, 4 (1.5 per cent) because of embryonic mortality, and 10 unaccountably disappeared (possibly removed by the female). Thus, total loss from non-hatched eggs amounted to 8.0 per cent. Saunders (1932), who suspected that the production of infertile eggs might be related to old age and highly nervous temperament of the laying female, found 14 (16.5 per cent) of 85 eggs observed to be infertile. The much higher percentage of infertile eggs in his study as compared to ours cannot at present be explained.

Factors Affecting Nest Success and Losses

Degree of nest construction.—Thinly- or non-roofed nests (61.8 per cent), in which the eggs were in some measure visible from above, suffered a 57.4 per cent loss to predation and were 33.1 per cent successful as compared to a 51.2 per cent loss and 38.1 per cent success for fully roofed nests. While not statistically significant ($P = 0.30$), these data at least suggest the possibility of greater risk of predation when eggs are visible from above. A further breakdown of these data show losses from predation to have been 60.5 per cent for open nests, 56.1 per cent for partially roofed nests, and 51.2 per cent for fully roofed nests.

Collias (1964) believed that the roofed nest, which probably evolved from a type that was open above, not only made predation less likely but also afforded cooler temperatures and protection from rain. Our data relevant to protection from heat and rain are too few to warrant discussion. However, the history of one open nest suggests the hardiness of eggs and young. Five birds successfully fledged from this unroofed nest which was located in vegetation less than 6 inches high. During the period when eggs were being laid and incubated, three daily rainfalls of 1.00, 0.58, and 0.11 inches were recorded; maximum air temperatures were 95°F or above on 6 days with a high of 97°. In the 12 days during which the young occupied the nest, three rainfalls

amounted to 1.38, 0.13, and 1.17 inches; temperatures were 90° or above on 6 days with a high of 96° recorded on 2 days.

Time of season.—Lanyon (1957), working with *S. magna* and *S. neglecta* in Wisconsin, reported a nesting success of 25.6 per cent for 86 nests of both species built during May and June and a 55.5 per cent success for 36 nests built during July and August. He suggested that higher nesting success during the latter part of the breeding season possibly reflected an increase in protective cover.

Data from our study also suggested an increase in nesting success as the season progressed. For comparative purposes, the season was divided into three parts: 14 April–26 May, 27 May–16 June, and 17 June–23 July. The per cent success of nests beginning in the above respective periods were 34.2, 37.9, and 55.6, while the percentages of nests destroyed by predators were 47.4, 43.9, and 27.8. Chi square in an $r \times 2$ contingency table was used to test whether the ratios of successful to preyed upon nests varied with the time of season. The value obtained (4.35) approached significance at the 10 per cent level. Nest losses attributable to causes other than predation (abandonment, mowing, etc.) remained fairly constant throughout the three periods at 18.4, 18.2, and 16.6 per cent, respectively.

Nolan (1963), analyzing the nesting success of 11 species of passeriformes, found that nest success increased significantly as the season progressed. He dismissed weather and nest abandonment as causes and stated: “. . . the rising rate of success as summer advances must presumably be attributed to some combination of differences in the activities, diets, numbers, or species of predators.”

As discussed earlier, skunks, house cats, dogs, and snakes were thought to have been the primary destroyers of meadowlark nests during our study. While no records were kept of their seasonal abundance and activities, some patterns were apparent from general observations. It is doubtful that the hunting habits of domestic dogs and cats varied greatly during the course of the nesting season. Snakes, on the other hand, were seen with increasing frequency during May, becoming progressively more scarce in June and July. This agrees with the observations of Klimstra (1958) in Davis County, Iowa. Conversely, skunks would logically be more numerous and active later in the season. Young skunks begin to hunt with the female at about 2 months of age, that is, sometime in July. Verts (1967) noted that female skunks were afield less during pregnancy and after it up to the time the young were about 1 month old; at that time (around 7–15 June), they resumed more or less normal nightly hunting patterns. Thus, observations of predator activities (with the exception of snakes) give no indication as to why predation should

be heavier early in the nesting season. In fact, contradictory evidence is available from Bobwhite nests located on the Research Area; these nests suffer significantly heavier losses to predators as the season progresses (Klimstra, unpublished data). At present, we have no explanation for these seemingly incompatible findings; there is nothing to suggest that Bobwhites and meadowlarks do not suffer nest losses from the various predators in relatively similar proportions. The whole problem of seasonal variation in nesting success is in need of further study.

Land-use types.—As already discussed, nests located on Bigler's pasture received unusually heavy losses from predation and, as this was thought to represent a special situation, the present section will deal only with nests located on other parts of the area. Nests in hayfields had the lowest rate of success (25.7 per cent); primarily this reflected losses to mowing (62.9 per cent). Nests in idle and fallow areas showed 29.6 per cent success with 63.0 per cent being destroyed by predators. Nests in pasture and soilbank fields had a success of 42.9 per cent and 50.0 per cent, respectively, while suffering losses to predation of 42.9 per cent and 45.0 per cent, respectively. Of the four nests located in wheat fields, three (75 per cent) were successful; however, the smallness of the sample prohibits concluding that these areas were relatively safer than others. The rate of abandonment was similar for all types of areas; 2.9 per cent in hayfields, 5.7 per cent in pastures, 5.0 per cent in soilbank fields, and 3.7 per cent in idle and fallow areas.

SUMMARY

From 1960 to 1967, 450 nests of the Eastern Meadowlark were found in the vicinity of Carbondale, Illinois. All nests were located at ground level and most were in cover 10 to 20 inches high; 17.3 per cent were open from above, 44.5 per cent were partially roofed, and 38.2 per cent had full canopies. The rush *Juncus*, meadow fescue, cheat, and bluegrass were most commonly used in nest construction. Almost 49 per cent of all nests faced in a general northeasterly direction.

Earliest date of egg laying was 14 April, the latest 23 July; peak egg laying occurred from 22 April to 12 May. Pastures showed the highest nest density per 100 acres with an average of 20.9, followed by hayfields 12.6, soilbank fields 5.1, wheat fields 4.8, idle areas 3.8, and fallow fields 2.0.

Average size of 101 complete clutches was 4.16 (range 2-6); number of eggs tended to decrease as the season progressed. Overall hatching success of 262 nests was 37.4 per cent; fledging success was 30.5 per cent. Predation (51.2 per cent) and mowing (12.2 per cent) were the primary destructive agents of nests. Extremely heavy losses to predators (72.2 per cent of 97 nests) in one field was discussed in detail. There appeared to be a direct relationship between degree of nest construction (amount of overhead protection) and nest success. The percentage of successful nests also increased as the season progressed.

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NEW LIFE MEMBER

Ralph W. Schreiber, a graduate student at Florida Southern University, has recently become a Life Member of the Wilson Society. Mr. Schreiber holds degrees from The College of Wooster, and The University of Maine. His major ornithological interest is the behavior-ecology of seabirds. His work on the Herring Gull was supported by a Louis Agassiz Fuertes Grant in 1966. Mr. Schreiber is a member of the AOU, the BOU, the Cooper Ornithological Society, and other scientific organizations.

DOMINANCE-SUBORDINATION IN CAGED GROUPS OF HOUSE SPARROWS

JOHN R. WATSON

ORNITHOLOGISTS long have been intrigued with the behavioral mechanisms which tend to promote gregariousness and precision of flock activities (Emlen, 1952; Moynihan, 1960; Crook, 1961). Dominance-subordination relationships in gregarious species have been studied by a number of workers (Masure and Allee, 1934; Shoemaker, 1939; Ritchey, 1951; Sabine, 1959; Thompson, 1960; and Ellis, 1966) to name but a few.

The behavioral mechanisms operating in the maintenance of gregariousness in the House Sparrow (*Passer domesticus*) have received little attention. The possibility that dominant individuals act to synchronize group activities in large foraging flocks of House Sparrows was suggested by Summers-Smith (1963). Some aggressive characters in a flock of color-marked House Sparrows were studied by Simmons (1954) but he made no statements on the dominance structure of the flock.

Since this species occurs commonly in large flocks, observations of dominance-subordination relations and behavioral cycles are made difficult by the diversity of flock activities. However, if a dominance structure exists, it should be evident in small flocks subjected to intensive study. Accordingly, groups of House Sparrows were assembled in order to study the various aspects of dominance-subordination under captive conditions.

METHODS

Eight groups of House Sparrows totaling 52 individuals were taken at various locations in and around Logan, Utah, between January and September, 1965. The groups contained 8, 8, 4, 6, 6, 8, 6, and 6 individuals, respectively. No more than two individuals of any group were taken from any one locality, thus minimizing the influence of previous interactions. Excepting one group (Table 2), no individual was used in more than one experiment. Members of each group were individually color marked and released into the aviary simultaneously. Two separate, visually isolated aviaries measuring $9 \times 7 \times 10$ feet were utilized in the study.

Constant 12-hour photoperiods were maintained through the use of an automatic light timer installed after April, 1965. Observations were made through tinted glass.

Each aviary was supplied with a perch graduated at one-inch intervals, a simulated tree perch, a water can, and a large floor feeder (a wooden tray, 18×36 inches). Millet was provided ad libitum and meal worms (*Tenebrio*) were occasionally used.

The observation periods were rotated daily on a systematic basis ("morning," "afternoon," and "evening") in order to compensate for cyclic behavior fluctuations.

Both first-year and juvenile birds were included in this study (Table 1, groups 3, 4, 6.

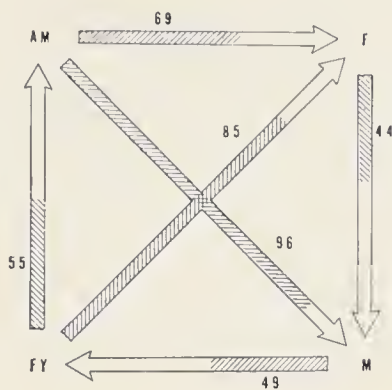


FIG. 1. Relative dominance between four classes of House Sparrows. Cross-hatching indicates the percentage of encounters won. For example, first-year birds were dominant to adult females in 85 per cent of the contests. Based on the dominance-subordination data from groups 1-7 (Table 1). Key: AM—Alpha Male; F—Adult Female; M—Adult Male; FY—First-Year (A composite of first-year and juvenile birds).

and 7). First-year birds are those which completed the post-juvinal molt and still show incomplete skull ossification. However, I will refer to both age classes as first-year birds; exact designation will be given in the tables.

Social ranking was determined through dominance and subordination responses (i.e., supplanting by the dominant bird and subsequent withdrawal by the submissive) at the feeder, water can, and perches. Threat displays resulting in spacing were not recorded as a "win" or "loss." Dominance and subordination were tested using the chi-square test with a 2×2 contingency table (Ostle, 1963). The correction for continuity was used on 2×2 tables. The percentages of wins were compared for each bird in each group.

Additional information was obtained by observing free-living flocks of House Sparrows at two locations outside Logan, Utah, from March, 1965, through September, 1965. One flock numbering around 100 individuals contained 37 marked birds.

RESULTS

Dominance and subordination.—The general pattern of interactions is shown in Figure 1. Each group under observation included a dominant adult male (Tables 1-2). Although no straight-line social rank system was present, I will refer to the individual having the highest number of wins as the alpha male. Due to the presence of this more combative bird (see beyond), all groups were highly significant (99 per cent level) with respect to the percentages of wins. Analysis showed significant differences (95 per cent level) between this more combative bird and other flock members. Three exceptions occurred (Table 1, groups 3 and 4; Table 2, 8b, 8c, and 8e). Groups 3 and 4 (Table 1) included first-year birds. First-year males secured high percentages of wins through successful encounters with the alpha male (Figure 1, Table 4). Simons (1954) stated that he found "juvenile" House Sparrows to be regularly very pugnacious over food, holding their own not only with adult House Sparrows but sometimes against Starlings (*Sturnus vulgaris*). Similarly, Thompson

TABLE 1
THE PERCENTAGES OF WINS OF 7 GROUPS OF CAPTIVE HOUSE SPARROWS

Groups	Alpha Male	Male	Male	Male	Female	Female	Female	Female
1 2-29 January 1965								
Per cent of Wins	85 (843)	41* (285) ¹	14* (319)	9* (282)	64* (160)	67* (135)	33* (151)	16* (153)
2 6-19 February 1965								
Per cent of Wins	92 (472)	14* (367)	34* (121)	24* (144)	50* (70)	52* (48)	33* (57)	49* (35)
3 1-20 April 1965								
Per cent of Wins	93 (378)	38* (164)	11* (372)	fy ² 67* (30)	sfy ² 56* (36)	17* (12)	— —	— —
4 7-22 May 1965								
Per cent of Wins	87 (198)	15* (124)	32* (66)	fy ² 64 (58)	20* (35)	8* (39)	— —	— —
5 9 June-6 July 1965								
Per cent of Wins	83 (551)	11* (311)	41* (169)	36* (100)	34* (86)	40* (62)	40* (60)	29* (21)
6 30 July-18 August 1965								
Per cent of Wins	84 (306)	44* (122)	12* (177)	juv ² 56* (104)	20* (49)	4* (46)	— —	— —
7 11 September-4 October 1965								
Per cent of Wins	82 (319)	30* (233)	40* (154)	juv ² 94 (137)	15* (59)	69* (118)	— —	— —

¹ Number in parentheses is the size of sample.

² fy = first year; sfy = suspected first year; juv = juvenile.

* Significant differences from Alpha Male (0.95 level).

(1960) stated that in the wild, "juvenile" House Finches (*Carpodacus mexicanus*) often won encounters over adults of the same species. Inspection of groups 3 and 4, and 7 shows high percentages of wins for the first-year birds relative to the alpha male. However, marked differences occur when one compares the total number of encounters between the two birds (alpha and first-year). Therefore, regardless of this result, the alpha male was still the more combative bird.

TABLE 2
CUMULATIVE PERCENTAGE OF WINS OF 2 GROUPS OF CAPTIVE HOUSE SPARROWS

Groups	Male (A)	Male (B)	Male (C)	Male (D)
8a. 23-28 April 1965				
Percentage of wins	76*	24**	—	—
8b. First two hour observation period, 29 April 1965, males C and D are from group three (Table 1) having previous win-loss ratios of 0.9259 and 0.1129 respectively.				
Percentage of wins	92*	100	4**	0**
8c. Second two hour observation period on 30 April 1965				
Percentage of wins	69	100	50	0
8d. Third two hour observation period on 1 May 1965				
Percentage of wins	23**	0**	96*	0**
8e. Fourth hour observation period on 2 May 1965				
Percentage of wins	25**	100	76*	0**

* Denotes alpha male.

** Significant difference from alpha male (0.95 level).

Characteristically, the alpha male initiated the aggression against the first-year birds. Once attacked, the first-year males—and in one case a suspected first-year female (Table 1, group 3; Table 3)—demonstrated marked abilities of self-defense, often assuming the hen threat posture illustrated by Summers-Smith (1963, Fig. 2). The first-year birds never pressed the attack, but merely refused to leave their positions even if actual fighting contact occurred. Similar behavior occurs in Blue Tits (*Parus caeruleus*) in which feeding birds show a tendency to stay and threaten intruders in lieu of overt attack (Stokes, 1962). Uinta ground squirrels (*Citellus armatus*) involved in maintenance activities also demonstrated this “stay threat” behavior (Balph and Stokes, 1963). “Stay threat” behavior was more pronounced in juvenile ground squirrels than adults (Balph, personal communication). Also, “stay threat” response was more intensely displayed by first-year House Sparrows than by adults of the same species.

The alpha male defended the simulated tree perch, the marked perch, and the elevated water can. At night the remaining males were forced to use the floor or to cling to the tiled ledges for perch (roost) sites. The females and first-year birds generally roosted on the floor but sometimes they remained on the elevated perches with the alpha male.

Examination of Tables 3 and 4 shows the alpha male directing a great number of attacks toward one specific adult male. This male maintained no spe-

TABLE 3
INDIVIDUAL ENCOUNTER DATA FROM THE APRIL GROUP (TABLE 1, GROUP 3)

Bird	Alpha Male A	Male B	Male C	First Year Male D	First Year Female E	Female F
			Loss			
A		66	268	4	10	2
B	6		56	0	0	0
C	0	34		4	2	2
Win						
D	6	2	2		4	6
E	14	0	4	2		0
F	2	0	0	0	0	

cific site and thus was subject to constant attacks from the alpha male. The remaining adult males secured isolated sites at which they remained (unless feeding or drinking), and which they actively defended. These sites were not associated with any perching device in the aviary but were situated in the far left corner (from entrance) of the aviary 75 inches from the floor level on a ledge atop the tiled portion of the wall. The adjacent right corner was only 6 inches from the elevated perch and hence was defended by the alpha male. At these specific sites, the alpha male was subordinate.

In groups 1, 2, and 5 (Table 1) the site problem was more acute due to the presence of four adult males. In each of these groups, an adult male remained on the wall thermostat which was situated only two feet from the elevated perch. This position offered some protection from the alpha male and usu-

TABLE 4
INDIVIDUAL ENCOUNTER DATA FROM THE AUGUST GROUP (TABLE 1, GROUP 6)

Bird	Alpha Male A	Male B	Male C	First Year Male D	First Year Female E	Female F
			Loss			
A		56	140	24	22	14
B	22		6	10	10	6
C	2	8		4	0	8
Win						
D	26	4	9		8	9
E	0	0	0	0		2
F	0	0	2	4	4	

ally ensured its occupant of an elevated roost overnight. Again, the male receiving the majority of defeats had no specific site to defend.

The flocks tended to remain in only one half of the aviary even though perching devices were placed at the opposite end. The area in which the flocks remained contained the food and water trays. Birds flying to the far end of the aviary were quick to return to the flock. Similar behavior was reported for *Quelea quelea* by Crook (1961). The subordinate males did not utilize the far corners for roost sites. Seemingly, the attraction of the group had priority over the effects of subordination.

Status of females and first-year birds.—As shown in Figure 1, adult females were subordinate to the other classes of sparrows. This was due, in part, to their tendency of readily submitting to aggression on the perches. The females initiated few direct agonistic encounters. Their fights per hour averaged 1.3, whereas adult males averaged 8.2 fights per hour. This last figure is somewhat distorted, however, due to the activity of the alpha male. Normally, males would not attack females unless they crowded too close on the perches or in the feeder. Attacks upon females by males were of low intensity and rarely included physical contact. Many times the females would merely space out, this action being sufficient to halt the male aggression. However, adult females were dominant over adult males in 44 per cent of the encounters (Fig. 1). In contrast, male attacks upon males invariably necessitated one or the other leaving the immediate site. The first-year birds tended to remain with the adult females and were treated as females by adults of both sexes.

The alpha male characteristically made direct, sudden attacks upon the adult males with little preliminary display given. However, his attacks upon females and first-year birds were of a threat nature, followed by direct attack only if the recipient failed to respond by moving away or by showing submissive behavior.

Because they had not yet completed the post-juvinal molt, the juveniles (Table 1, groups 6 and 7) closely resembled the adult females in appearance and (as indicated above) were treated as adult females. This similarity of juvenal plumage to that of advanced first-year or adult female House Sparrows has been described by Selander and Johnston (1967). The two first-year males (Table 1, groups 3 and 4) showed a variable amount of white tipping to the black chin feathers, and the pileum had a brownish hue, rather than gray of the adult male.

As stated previously, "stay threat" behavior was characteristic of both juvenile and first-year birds. The results of "stay threat" are reflected in the high win success as indicated in Figure 1. This pugnacity seems functional, for these young birds can defend against intruding adult males while feeding and

perching. These early aggressive encounters undoubtedly contribute to the fitness of young birds by providing valuable fighting experience prior to their first breeding season.

Manipulation of birds.—One experiment was conducted with two males designated A and B, respectively. A was dominant over B (Table 2, 8a) having 59 wins to 19 wins for B. On 20 April 1965, I released two birds from the April group, the alpha male designated C and a subordinate male designated D (Table 1, group 3) with A and B. During the first two hours of observation, A defeated C 94 times, illustrating how familiarity with an area can influence the outcome of aggressive encounters. Similar results were reported for caged groups of House Finches by Thompson (1960). D, who had lost all previous encounters with C, was successful in defeating C 19 times on the perches. Two factors seemed to be involved. When the alpha male would rapidly displace one individual about the aviary, others might also join in and displace the recipient. The recipient, under these conditions, would readily give way to any aggression directed towards him. There seemed to be an “aggressive momentum” operating first in the attack by the alpha bird, and subsequently spreading to the other flock members. Correlated with this was a tendency towards heightened submission by the bird subjected to these rapid attacks. Another factor was that C, who previously had maintained a large defended area, now was without one in strange territory.

On the third day, C was ahead of A with percentages of 96 and 23, respectively, indicating a reversal of dominance (Table 2, 8d). This relationship held until the sixth day, when A was discovered dead.

Flock activities.—Within certain limitations, synchronization and integration within the flocks followed an intrasexual pattern. However, the first-year birds tended to remain with the adult females and were treated as females by adults of both sexes. Figure 2 represents a sample recording of group activity cycles from a well-stabilized flock at four times over the course of one photoperiod. The figures show that the individuals tended to be engaged in the same activities at the same time, much as shown for *Quelea quelea* by Crook (1961).

Despite uniformity of photoperiod (constant 12 hr) and temperature, a definite daily activity pattern was present. Figure 2 illustrates this phenomenon. The greatest amount of active behavior (e.g., feeding) occurred in “morning” and “evening” periods, whereas the “afternoon” period was characterized by drowsiness with much sitting and occasional feeding. These patterns resembled those described by Beer (1961) for free-living winter flocks of House Sparrows. The last half-hour of light was one of great vocal and aggressive activity resembling natural pre-roosting behavior. Although these be-

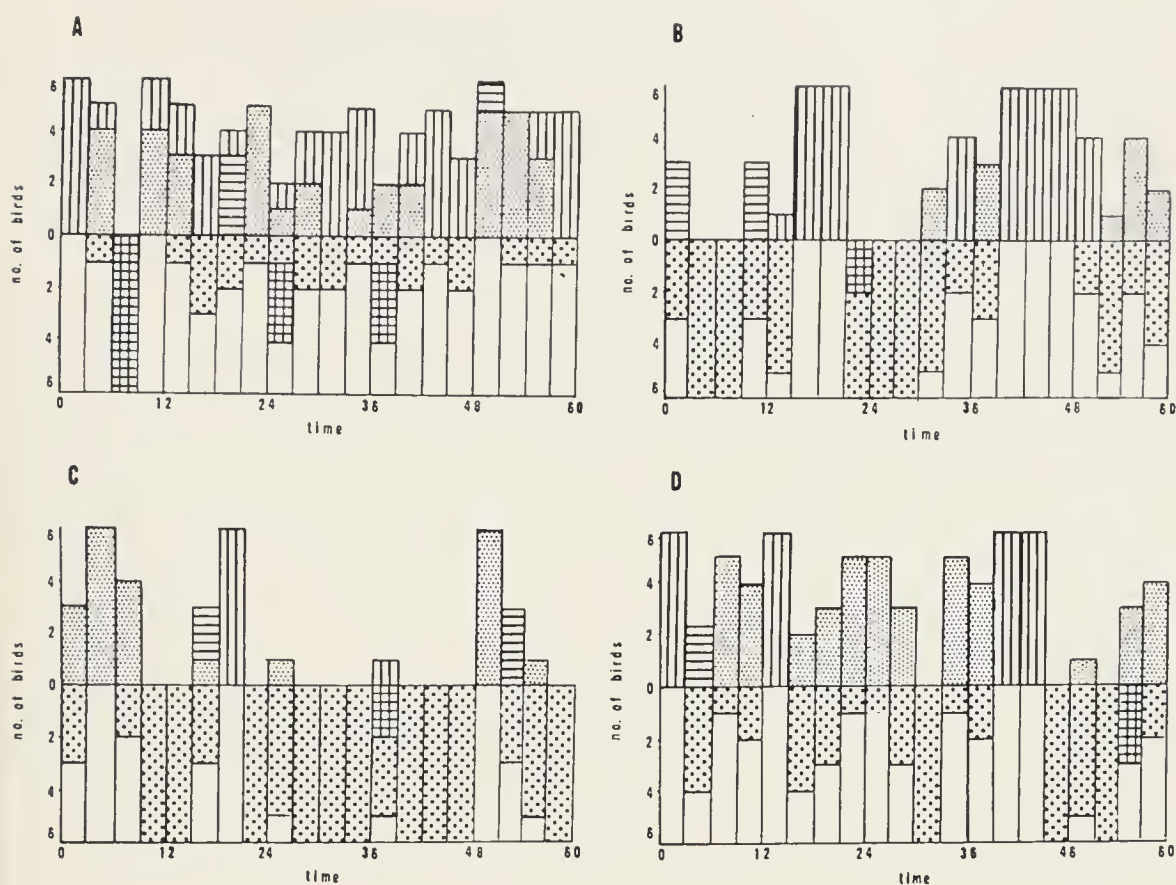


FIG. 2. Recording of group activity cycle of House Sparrows from the June-July flock (Table 2, group 5). Six birds observed for 60 minutes from 07:00-08:00. (A), 10:30-11:30. (B), 13:30-14:30. (C), 17:00-18:00. (D). Observations were made at the beginning of each three minute period. Key: Feeding—Small dots; Hopping—Horizontal bars; Flying—Vertical bars; Sitting—Large dots; Feather care—Cross bars.

havioral adjustments were made under artificial conditions, they served to establish a cyclic context from which observations could be interpreted. As stated by Moynihan and Hall (1953), the motivation of a specific behavior pattern was considered to be the same, whether performed in a cage or in the wild.

In these experiments, the alpha male showed a marked tendency to divorce himself from flock activities. This bird showed little tendency to follow others and no marked potential for initiating new flock activities. When not fighting, the alpha male could be identified by his behavior of sitting lethargically in one place and not participating in flock activities.

Data from the April group (Table 2, 8a) showed A dominant over B. Out of 226 flights by A, individual B followed 158 times. Conversely, out of 606 flights by B, male A followed only 32 times. The greater number of flights by B was attributed to the great nervousness of the bird. In this case, the sub-

ordinate did follow the alpha male a significant number of times. However, this was probably the result of a small opportunity for alternate action coupled with the nervousness of B. Also, the passive behavior of the alpha male was a factor. In larger groups ($N = 6$ to 8), all birds showed an equal potential for elicitation of new activities (based on qualitative notes).

DISCUSSION

The dominance-subordination relationships of highly gregarious species of birds have been subject to much speculation. Schjelderup-Ebbe (1933) stated that beyond 10 individuals, straight-line hierarchies rarely exist. Conversely, Guhl (1953) gave evidence for a hierarchy in a flock of 96 pullets. Sabine (1959) described a scale of dominance for a flock (that resulted from the amalgamation of two flocks) of 42 Oregon Juncos (*Junco oreganus*). However, it would seem that these flock sizes represent the extreme upper limits for individual meeting and acquaintance to occur.

Whether the results of investigations using small numbers apply equally well to larger flocks was questioned by Banks and Allee (1957). It seems reasonable, however, that if a hierarchy is nonexistent in small flocks one would not exist in larger flocks of the same species.

No obvious linear hierarchy existed with the captive sparrows. For example, Table 3 (April group) indicates a peck rank for three adult males (A 66/72, B 6/72, C 0/268). The disproportionate defeats assumed by C were due to his lack of a defended site. However, B, who did maintain a specific site at which he remained, was largely free from attacks and managed to defeat A 6 times at this location. Therefore, the situation revealed reversible site-related dominance among the males. Since the black bill color was lost by the captive males indicating gonadal regression (Keck, 1932) and no sexual displays were seen, reproductive complications were minimized.

Instances of caged birds establishing separate territories have been recorded for a few species (Shoemaker, 1939; Ritchey, 1951). In caged groups of House Finches, the alpha pair defended the entire aviary with the beta pair defending the same area but with less aggressiveness (Thompson, 1960). However, Ellis (1966) showed a hierarchy independent of site relationships in captive groups of Starlings. In my experiments, the alpha male exerted his influence over the largest area somewhat resembling the behavior of the caged House Finch but the sparrow aggression was not related to pair nest defense, and the other male sparrows did not defend the same area. The situation seemed to agree with the findings of Ritchey (1951) who stated that in caged groups of domestic pigeons, a linear hierarchy was blocked by site-related dominance.

The results of this captive study may relate to certain events occurring under natural conditions. As stated by Dixon (1965), reversible, site-related responses between individuals have little value in promoting group unity. Free-living adult male sparrows maintain one specific site for both the breeding and non-breeding season (Summers-Smith, 1963). However, the intensity of intolerance exerted in defense of these sites during the non-breeding season is unclear. In any event, this type of site-related aggression would have questionable significance in large flocks of foraging sparrows. When on neutral ground, an attacking sparrow seems to have the advantage over the recipient (notwithstanding "stay threat" behavior). This situation was apparent in the large floor feeder where aggression was rare. Reduced aggression at the feeder has also been reported for caged groups of Goldfinches (*Spinus tristis*) by Coutlee (1967).

SUMMARY

Dominance-subordination relationships were studied in 8 groups (2-8 individuals per group) of captive House Sparrows between January and September, 1965. In each group a highly combative male won the majority of contests, but a linear hierarchy was blocked by reversible site-related dominance. The significance of site-related aggression in large flocks of foraging House Sparrows is questioned. The adult females rarely fought among themselves and were largely free from adult male aggression. First-year birds were treated as adult females by adults of both sexes. However, when attacked they demonstrated "stay threat" behavior. "Stay threat" was characterized by the first-year birds actively defending their positions when attacked without pressing the encounter beyond the immediate site.

Activity patterns were greatest during "morning" and "evening" periods with a characteristic "mid-day lull." The birds tended to engage in the same activities at the same time. The top-ranking adult male showed a tendency to divorce himself from the flock and demonstrated no marked potential for initiating new flock activities.

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AVIAN BILL-WIPING

GEORGE A. CLARK, JR.

THIS first review of the taxonomic distribution of bill-wiping was undertaken to determine whether occurrence of this trait might aid in clarifying evolutionary and systematic relationships among higher categories of birds. Sources of data are my field observations of bill-wiping in 27 passerine species and the cited publications. Although hundreds of papers were consulted, some records of bill-wiping have undoubtedly been missed.

Bill-wiping typically involves rapid withdrawal of the side of the beak from base to tip closely adjacent to a foreign surface such as a branch or the ground. Excluded from consideration is wiping effected as the bill touches other parts of the body or that of another bird; such contacts are not usually described as bill-wiping.

Wiping varies in detail even for an individual bird at different times. Many kinds of structures provide wiping surfaces; I have seen passerines wipe on rope clothesline, fence wire, the edge of a metal birdbath, and the rim of a metal incinerator. Birds may or may not be perched on an object upon which they wipe, e.g., they may sit on one branch yet wipe on another nearby. If both sides of the bill are wiped in a single session, the sides are usually alternated. The number of wipes per session also varies widely (Morris, 1957*a*); the maximum rate reported is 90 wipes in a few minutes by the estrildine *Poephila bichenovi* (Morris, 1957*b*). Details of wiping are often difficult to see in the field. It is reported that the bill may be open or closed during wiping (Dunham, 1966*a*). Moreover, the bill reportedly often does not contact the object adjacent to which it is "wiped" (Hinde, 1953; Morris, 1954). If the bill fails to touch, the term "wiping" is misleading in a literal sense but still descriptively convenient. Despite its many variations, bill-wiping appears on the whole to be a distinctive and readily recognizable behavioral characteristic. Hinde (1953) and Hardy (1963) have published illustrations of bill-wiping.

FUNCTION

As judged from its frequency and the component movements of head, neck, trunk, and legs, bill-wiping involves cumulative expenditure of substantial time and energy. It therefore seems likely that such bill-wiping is selectively advantageous, even though the benefits are frequently obscure.

Cleaning.—As widely noted, birds frequently bill-wipe after eating messy foods such as suet, fruits, or juicy insects. Such wiping presumably aids sanitation and may help to maintain bill mobility and streamlining.

Those species not bill-wiping presumably use alternate ways of bill-cleaning, e.g., rubbing the bill on feathers or feet, pushing the bill into sand or other material, scratching with the foot, head shaking, and bathing. The cleaning methods appear to be effective, for free-living birds with conspicuously dirty bills are uncommon.

Honing.—Hardy (1963) notes for the parrot *Aratinga canicularis* that wiping may have a honing function, as wiping is sometimes done, evidently deliberately, on rough barked trees. A scraping noise heard during bill-wiping by the Rose-breasted Grosbeak (*Pheucticus ludovicianus*; Dunham, 1966a) might indicate substantial contact of the bill in wiping. However, in examining bills of study skins of various passerines with a binocular dissecting microscope, I find no clear evidence of the effects of wiping.

If bill-wiping serves in honing, it would seem essential that the bill grow sufficiently rapidly to offset wear through honing. Hypothetically one would expect selection to yield growth patterns not requiring special wiping to maintain or produce normal bill shapes. Unfortunately, not enough is known to correlate bill growth with bill-wiping, although there is much evidence that bills are continually growing and wearing away (Davis, 1954; Witschi and Woods, 1938; Wydoski, 1964). Wiping, serving primarily other functions, presumably produces some wear.

As judged from data assembled by Pomeroy (1962) on bill abnormalities, the frequency of malformed bills is not correlated with the occurrence or absence of bill-wiping.

Displacement activities.—Birds often bill-wipe without apparent debris on the bill and not immediately after feeding, bathing, drinking, or manipulation of objects with the bill. Indeed, as noted above, in some cases the bill reportedly does not contact the object against which it is "wiped" (cf. Morris, 1954). Much wiping thus meets a standard criterion for displacement activities in being seemingly irrelevant in a particular behavioral context.

It is difficult to categorize adequately the variety of situations in which displacement bill-wiping occurs. In a common case, a bird feeding on the ground is flushed by another bird or person and after flying to a branch engages in bill-wiping. Wiping movements occur frequently during agonistic behavior (see Coutlee, 1967; Dunham, 1966b; Nero, 1963). Furthermore, wiping may take place during predominantly sexual behavior as reported by Coombs (1960), Morris (1954), Moynihan (1963), and Summers-Smith (1963:24–25). Nice (1943:40) and Reiskind (1965) give examples of bill-wiping following contact with, or manipulation of, distasteful objects. Many of the foregoing examples involve situations in which birds are seemingly thwarted from completing an activity; however, some displacement wiping is associated with

transitions between activities without apparent thwarting. For example, I have observed a male Yellowthroat (*Geothlypis trichas*) fly to a branch, bill-wipe, and then begin to sing. Still other cases of wiping do not appear to involve thwarting, transition in activities, or cleaning. As examples, I have seen both the Yellow Warbler (*Dendroica petechia*) and the Prairie Warbler (*D. discolor*) bill-wipe during pauses in periods of singing. As Brown (1964) points out, the factors eliciting displacement bill-wiping may be very subtle so that detecting them in the field is often difficult or impossible.

That not all bill-wiping is a form of bill maintenance (i.e., cleaning or honing) is suggested by wiping without contact and also by intraspecific variations in frequency of wiping according to social rank or sex. Stokes (1963:13) observed more wiping in subordinate than in dominant partridges (*Alectoris*). In contrast, Hinde (1953) found bill-wiping commoner in dominant than subordinate Chaffinches (*Fringilla coelebs*). Morris (1954) recorded a higher frequency of bill-wiping by males than females during precopulatory displays of *Poephila guttata*. The selective advantages in bill-wiping and other displacement activities are relatively unstudied but may involve changes in the physiological state of the bird and in its responsiveness to environmental stimuli (cf. Rowell, 1961; Delius, 1966). It is curious that possible changes in internal state should be linked with such extensive body movements.

SYSTEMATIC SURVEY

Table 1 is a summary of species for which bill-wiping has been reported. For most species existing records of bill-wiping are fragmentary relative to the variety of contexts in which wiping may potentially occur. It is therefore premature to categorize species according to occurrence or frequency of bill-wiping in particular behavioral contexts. However, interspecific variations of this kind may occur widely. For example, Morris (1957*b*) found that *Lou-chura cucullata* frequently preens as a displacement activity in contexts in which other estrildines show displacement bill-wiping.

Probably all groups listed in Table 1 bill-wipe as a means of cleaning the bill, but bill-wiping as a displacement activity has thus far been reported apparently for only Phasianidae, *Larus ridibundus*, Psittacidae, and many passerines. The wide distribution of bill-wiping in parrots and passerines suggests that wiping may be characteristic for these two orders.

I have found a few negative reports. Bill-wiping on a branch is unrecorded in waterfowl (Anatidae) despite arboreal perching by some species (McKinney, 1965:181). Variation in occurrence of wiping exists within the family Laridae. Tinbergen (1959:18, 52) notes that, when visited by a female, a male Black-headed Gull (*Larus ridibundus*) may peck at the ground and then bill-wipe.

TABLE 1
RECORDS OF BILL-WIPING

Family	Species	Reference
Tinamidae	<i>Nothoprocta cinerascens</i>	Lancaster, 1964: 280
Ardeidae	<i>Butoroides virescens</i>	Meyerriecks, 1960: 11
Tetraonidae	<i>Lagopus scoticus</i>	Watson and Jenkins, 1964: 146
Phasianidae	<i>Alectoris</i> sp.	Goodwin, 1953; Stokes, 1963
	<i>Gallus gallus</i>	Nice, 1962: 81
	<i>Colinus virginianus</i>	Nice, 1943: 40
Laridae	<i>Larus ridibundus</i>	Tinbergen, 1959
Psittacidae	<i>Aratinga canicularis</i>	Hardy, 1963
	<i>Brotogeris jugularis</i>	Power, 1967
	<i>Loriculus galagulus</i>	Buckley, 1968
	<i>L. vernalis</i>	" "
	<i>Melopsittacus undulatus</i>	Brockway, 1964
Picidae	<i>Colaptes auratus</i>	Kilham, 1959
	<i>Sphyrapicus varius</i>	Kilham, 1962; Lawrence, 1967: 120
Formicariidae	<i>Gymnopithys</i> , 3 species	Willis, 1967, 1968
Tyrannidae	<i>Empidonax traillii</i>	this study
Hirundinidae	<i>Iridoprocne bicolor</i>	" "
Corvidae	<i>Cyanocitta cristata</i>	Hardy, 1959; this study
	<i>C. stelleri</i>	" "
	<i>Aphelocoma caerulescens</i>	" "
	<i>A. ultramarina</i>	" "
	<i>Calocitta formosa</i>	" "
	<i>Corvus frugilegus</i>	Coombs, 1960
Paradisaeidae	<i>Parotia carolae</i>	Frith, 1968
	<i>Paradisaea raggiana</i>	Rand and Gilliard, 1968
Paridae	<i>Parus atricapillus</i>	Reiskind, 1965
	<i>P. carolinensis</i>	Brewer, 1961
	<i>P. major</i>	Howard, 1951
Troglodytidae	<i>Troglodytes troglodytes</i>	Armstrong, 1955: 30
	<i>Campylorhynchus</i> <i>brunneicapillus</i>	Ricklefs, 1966
	<i>Mimus polyglottos</i>	this study
Mimidae	<i>Dumetella carolinensis</i>	" "
	<i>Toxostoma curvirostre</i>	Ricklefs, 1966

TABLE 1 cont.

Family	Species	Reference
Turdidae	<i>Erithacus rubecula</i>	Mostler, 1935
	<i>Luscinia megarhynchos</i>	" "
	<i>Phoenicurus phoenicurus</i>	" "
	<i>Sialia sialis</i>	this study
	<i>Saxicola rubetra</i>	Mostler, 1935
	<i>Turdus migratorius</i>	this study
Sylviidae	<i>Hippolais icterina</i>	Mostler, 1935
	<i>Sylvia atricapilla</i>	" "
	<i>S. communis</i>	" "
Muscicapidae	<i>Ficedula hypoleuca</i>	" "
Bombycillidae	<i>Bombycilla cedrorum</i>	this study
Laniidae	<i>Lanius excubitor</i>	Cade, 1962
	<i>L. ludovicianus</i>	Miller, 1931: 220-221
Sturnidae	<i>Sturnus vulgaris</i>	this study
Vireonidae	<i>Vireo bellii</i>	Nolan, 1960
	<i>V. olivaceus</i>	this study
Parulidae	<i>Dendroica petechia</i>	" "
	<i>D. kirtlandii</i>	Mayfield, 1960: 66
	<i>D. discolor</i>	this study
	<i>Seiurus aurocapillus</i>	" "
	<i>Seiurus</i> sp.	" "
	<i>Geothlypis trichas</i>	" "
	<i>Setophaga ruticilla</i>	Ficken, 1962
Ploceidae	<i>Poephila guttata</i>	Morris, 1954
	<i>P. bichenovi</i>	Morris, 1957b
	<i>Lonchura cucullata</i>	" "
	<i>L. punctulata</i>	Moynihan and Hall, 1954
	<i>L. striata</i>	Eisner, 1960
	<i>Ploceus</i> (= <i>Sitagra</i>) <i>melanocephalus</i>	Crook, 1963
	<i>Passer domesticus</i>	Summers-Smith, 1963; 24-25; this study
	Icteridae	<i>Xanthocephalus</i> <i>xanthocephalus</i>
<i>Agelaius phoeniceus</i>		" " ; this study
<i>Icterus galbula</i>		this study
<i>Quiscalus quiscula</i>		Ficken, 1963; this study
<i>Molothrus ater</i>		Nicc, 1943; Nero, 1963; this study

TABLE 1 cont.

Family	Species	Reference
Thraupidae	<i>Habia rubica</i>	Willis, 1960
	<i>H. gutturalis</i>	" "
Fringillidae		
Richmondinae	<i>Pheucticus ludovicianus</i>	Dunham, 1966a, 1966b; this study
Emberizinae	<i>Arremonops conirostris</i>	Moynihan, 1963
	<i>Junco hyemalis</i>	this study
	<i>Spizella arborea</i>	" "
	<i>S. passerina</i>	" "
	<i>Melospiza georgiana</i>	" "
	<i>M. melodia</i>	Nice, 1943: 21, 34; this study
Carduelinae	<i>Fringilla coelebs</i>	Hinde, 1953; Rowell, 1961
	<i>F. montifringilla</i>	Hinde, 1955-56
	<i>Serinus</i> sp.	Nice, 1943: 40; Hinde, 1955-56; Vince, 1961
	<i>Chloris chloris</i>	Hinde, 1955
	<i>Carduelis carduelis</i>	Hinde, 1955-56
	<i>Spinus tristis</i>	Coutlec, 1963, 1967
	<i>Acanthis flammea</i>	Dilger, 1960
	<i>Carpodacus purpureus</i>	this study
	<i>Loxia curvirostra</i>	Tordoff, 1954
	<i>Pyrrhula pyrrhula</i>	Hinde, 1955-56
	<i>Coccothraustes</i>	
	<i>coccothraustes</i>	" "

Indeed, it regularly bill-wipes as a displacement activity, similar to the movements by which the bill is cleaned. This species thus differs from the Herring Gull (*Larus argentatus*) which tugs at vegetation rather than bill-wiping (Tinbergen, 1959). This constitutes an example of intrageneric variation in the occurrence of bill-wiping. Van Iersel and Bol (1958:7) in extensive observations of the terns *Sterna hirundo* and *S. sandvichensis* saw no bill-wiping.

For the majority of families there are neither positive nor negative records. In watching such species as Killdeer (*Charadrius vociferus*), Rock Doves (*Columba livia*), and Mourning Doves (*Zenaidura macroura*), I have failed to see bill-wiping, but further data are needed. Present negative evidence suggests that bill-wiping is absent, or occurs rarely, in a variety of waterbirds.

Another questionable group is the Trochilidae. DuBois (1938) reports an

TABLE 2
EARLIEST APPEARANCE OF BILL-WIPING IN SOME PASSERINE SPECIES

Species	Days Posthatching	Reference
<i>Cyanocitta cristata</i>	15	Hardy, 1959
<i>Campylorhynchus brunneicapillus</i>	24	Ricklefs, 1966
<i>Toxostoma curvirostre</i>	16	" "
<i>Lanius ludovicianus</i>	33	Miller, 1931: 220-221
<i>Setophaga ruticilla</i>	8	Ficken, 1962
<i>Molothrus ater</i>	14	Nice, 1943: 40
<i>Pheucticus ludovicianus</i>	7-11	Dunham, 1966a
<i>Melospiza melodia</i>	11	Nice, 1943: 21, 34
<i>Serinus canaria</i>	11 or earlier	Nice, 1943: 40

unsuccessful effort by a female Rufous Hummingbird (*Selasphorus rufus*) to wipe away a feather by rubbing her bill on the rim of the nest. After failing to dislodge the feather with her tongue, she eventually removed it by jabbing her bill downward into the nest. It is uncertain that the bill-wiping observed by DuBois corresponds to that of other birds.

EVOLUTIONARY INTERPRETATIONS

Although a few data are available on the ontogeny of bill-wiping (see Table 2 and the references cited therein), we know little about the possible roles of practice and learning in maturation of the trait. Nevertheless, in view of the absence of records of intraspecific variation in occurrence, the character appears to be species-specific and hence presumably strongly influenced genetically.

Clearly much more must be learned about the occurrence of bill-wiping before it can be broadly used taxonomically. Particularly needed are observations on the presence or absence of the trait in additional nonpasserine groups. Bill-wiping is a seemingly simple feature and hence may have been acquired or lost more than once in evolutionary history. However, bill-wiping appears to be as potentially suitable a taxonomic character as some simple, but widely cited, morphological ones (e.g., feathering of the oil gland; Clark, 1964).

As displacement activities are commonly believed to be a frequent evolutionary source for movements in stereotyped behavior, it would not be surprising if bill-wiping were found as a source in the evolution of certain displays. There are a few possible examples. Orians and Christman (1968:76) suggest that one possible source of the bill-down postures in certain icterids and ploceids might be bill-wiping (see also Mitchell, 1966). Moreover, the

sweeping movements of White-breasted Nuthatches (*Sitta carolinensis*) in possible chemical defense of nests against squirrels may have been derived from bill-wiping (Kilham, 1968).

SUMMARY

Bill-wiping is reviewed for Tinamidae, Ardeidae, Tetraonidae, Phasianidae, Psittacidae, Picidae, and 20 families of Passeriformes. Bill-wiping occurs in at least one, but not all, species of Laridae and has not been reported for Anatidae.

Functional interpretation of this behavior as a displacement activity remains uncertain. Bill-wiping appears to have moderate potential utility as a taxonomic character.

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EGG TEETH AND HATCHING METHODS IN SOME ALCIDS

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RECENT discussions on egg teeth (Wetherbee, 1959; Clark, 1961; Parkes and Clark, 1964) give little data on the Alcidae. While studying breeding biology of Parakeet (*Cyclorhynchus psittacula*), Crested (*Aethia cristatella*), and Least (*A. pusilla*) Auklets on St. Lawrence Island, Alaska, in 1966 and 1967, I had opportunity to observe egg teeth in several alcid species and hatching in the auklets and Horned Puffin (*Fratercula corniculata*). These observations are supplemented by examinations of alcid chicks in the American Museum of Natural History (AMNH) examined by C. E. O'Brien, Los Angeles County Museum (LACM) examined by K. E. Stager, National Museum of Canada (NMC) examined by W. E. Godfrey, San Diego Natural History Museum (SDNHM) examined by J. E. Jehl, Jr., University of British Columbia Museum of Zoology (UBCMZ), University of Michigan Museum of Zoology (UMMZ), United States National Museum (USNM) examined by R. C. Banks, and University of Washington Burke Museum (UWBM) examined by L. Spring. Specimens in UBCMZ and UMMZ were examined by myself.

ANNOTATED LIST

Alca torda.—Bédard (1969) reported the persistence of egg teeth in Razorbills up to the 14th day after hatching. Kartaschew (1960) and Perry (1940) figured egg teeth on the upper mandibles of this species. Chicks in SDNHM showed egg teeth on upper mandibles.

Uria aalge.—Tuck (1961) mentioned the presence of egg teeth in Common Murres; Perry (op. cit.) figured it in this species. One chick in NMC showed an egg tooth on the upper mandible only but some chicks of this species in SDNHM showed both upper and lower egg teeth.

Uria lomvia.—Tuck (op. cit.) mentioned the presence of egg teeth in Thick-billed Murres; Kartaschew (op. cit.) figured it in this species. Three chicks in NMC showed egg teeth on their upper mandibles only.

Plautus alle.—Bateson (1961) figured the egg tooth on the upper mandible of a Dovekie.

Cephus grylle.—Winn (1950) observed egg teeth becoming relatively smaller following hatching and disappearing between the 25th and 35th day after hatching. Kartaschew (op. cit.) figured egg teeth on the upper mandibles of Black Guillemots. Eight chicks in NMC showed egg teeth on their upper mandibles; one of these chicks has what looks like a very small remnant of an egg tooth on its lower mandible also (Godfrey, pers. comm.).

Cephus columba.—Thoresen and Booth (1958) figured the egg tooth of newly hatched Pigeon Guillemots and Drent (1961) observed it in chicks up to 28 days of age. On St. Lawrence Island, I observed two chicks which lost it between the 27th and 30th days after hatching. Two newly hatched chicks in UBCMZ show small, bilateral protuberances on their lower mandibles; these were undetectable in chicks of about two weeks of age

and older. Newly hatched Pigeon Guillemots in SDNHM also showed egg teeth on their lower mandibles.

Brachyramphus marmoratum.—Three chicks in UBCMZ and three in UWBM showed egg teeth on their upper and lower mandibles; each chick had fledged and was in juvenal plumage. Drent and Guiguet (1961) mentioned egg teeth being present on the upper mandibles of the UBCMZ specimens but did not mention egg teeth on their lower mandibles.

Brachyramphus brevirostre.—Thompson et al. (1966) figured and described the egg tooth on the upper mandible only in one chick. R. M. Mengel (pers. comm.) examined this specimen and reported an egg tooth-like structure also on its lower mandible; it takes the form of a double swelling with a slight trough separating the protuberances.

Endomychura hypoleuca.—Three chicks in AMNH and one in LACM show vestiges of egg teeth on their upper mandibles only. Chicks of this species in SDNHM show egg teeth on both mandibles and one chick in USNM which is labeled "just hatched" (Banks, pers. comm.) does not have an egg tooth on either mandible which indicates that it possibly fell off soon after hatching or during preservation.

Endomychura craveri.—Chicks in SDNHM showed egg teeth on their upper mandibles only; further observations are needed to establish the presence of egg teeth on their lower mandibles.

Synthliboramphus antiquum.—Drent and Guiguet (op. cit.) figured the egg tooth of this species. Newly hatched chicks in UBCMZ showed egg teeth on their upper and lower mandibles. Egg teeth on the upper mandibles in 11 chicks examined by me averaged 2.5 mm in diameter at their base.

Synthliboramphus wumizusume.—Three newly hatched chicks in UMMZ showed no egg teeth; however, each chick's label contains the notation "egg tooth white" (presumably referring to that on the upper mandible only). As in *E. craveri*, additional information is needed to establish the presence of egg teeth on their lower mandibles.

Ptychoramphus aleutica.—Thoresen (1964) figured the egg tooth on the upper mandible of a one-day-old chick; an 11-day-old chick showed no egg tooth. Egg teeth of nine newly hatched chicks in UBCMZ averaged 1.0 mm in basal diameter. Chicks in LACM, UBCMZ and SDNHM showed no egg teeth on their lower mandibles.

Cyclorhynchus psittacula.—The egg tooth, found only on the upper mandible, averages 1.5 mm in diameter at the base at hatching and gradually becomes smaller until it disappears between the 8th and 10th days after hatching.

Aethia cristatella.—Egg teeth of the upper mandibles average 2.4 mm in basal diameter and, like those of *C. psittacula*, become smaller and gradually disappear between the 8th and 10th days after hatching.

Aethia pusilla.—Egg teeth, on upper mandibles only, average 1.0 mm in basal diameter at hatching and persist up to about the 12th day after hatching.

Aethia pygmaea.—Two downy chicks in USNM showed egg teeth on their upper mandibles only.

Cerorhinca monocerata.—Four chicks in UWBM, two of them about one or two weeks old, do not have egg teeth. Richardson (1961) figured a four-week-old chick that did not have an egg tooth; three chicks about this age in UBCMZ also showed no egg teeth. Three chicks from pipped eggs in UWBM showed egg teeth on their upper mandibles only (L. Spring, pers. comm.) which indicates that egg teeth in this species are apparently lost within a week or two after hatching.

Fratercula arctica.—Kartaschew (op. cit.), Loekley (1953), and Myrberget (1959) figured the egg tooth on the upper mandible.

Fratercula corniculata.—I observed the persistence of an egg tooth on the upper mandible of a nestling on St. Lawrence Island up to the 29th day after hatching. The basal diameter of three egg teeth at hatching averaged 3.5 mm.

Lunda cirrhata.—Drent and Guiguet (op. cit.) figured the egg tooth of the upper mandible. Chicks in SDNHM showed egg teeth on their upper mandibles.

Each alcid species examined possessed an egg tooth on the culmen near the tip of the upper mandible; the absence of egg teeth on some chicks is probably attributable to loss during handling and preservation. This egg tooth does not encompass the entire tip of the mandible as is the case in scolopacids (Jehl, 1968). In *Cerorhinca monocerata* the egg tooth appears to be deciduous like that of scolopacids and apparently is lost soon after hatching. Chicks of *Brachyramphus marmoratum*, on the other hand, retain it until their juvenal plumage is assumed and they have fledged (see Drent and Guiguet, 1961:80). Egg teeth in auklets and probably most other alcids gradually disappear without, apparently dropping off abruptly.

Egg teeth or teeth-like structures were found on the lower mandibles of *Uria aalge*, *Cephus grylle*, *C. columba*, *Synthliboramphus antiquum*, *Endomychura hypoleuca*, *B. marmoratum*, and *B. brevirostre*. These egg teeth of lower mandibles of *Synthliboramphus* and *B. marmoratum* consist of thin, apparently calcareous, sheets that cover the entire tips of the mandibles. The egg teeth on the lower mandibles of *C. columba* and *B. brevirostre* differ in that they are in the form of a double, apparently bilateral, protuberance. The time of disappearance of this structure also varies; within a few days in *C. columba* and retained at least until the young have fledged in *B. marmoratum*.

Jehl (1968) discussed the apparent significance of the egg tooth, if it should be called such, of the lower mandible in scolopacids. He found no obvious role in hatching and stated that it may function to protect the delicate tip of the lower mandible during hatching. It is interesting to note that those alcids so far shown to possess an "egg tooth" on their lower mandibles have pointed bills with upper and lower mandibles being of nearly equal length. I have no observations on hatching in those species with egg teeth on their lower mandibles but in auklets, where egg teeth are present only on upper mandibles, the lower mandibles are not involved in hatching. It is possible that the function of the "egg tooth" on the lower mandibles of alcids with "pointed beaks" may be also of a protective nature.

The time between the occurrence of the first cracks on the shell and the emergence of the chick from the shell is variable in the auklets and Horned Puffin. This interval in four eggs of *C. psittacula* was two to four days (mean, 3.0 days), in eight eggs of *A. cristatella* was two to six days (mean, 3.3 days), in 27 eggs of *A. pusilla* was two to seven days (mean, 3.2 days), and in two eggs of *F. corniculata* was four to five days (mean, 4.5 days). In

hatching of auklets the first cracks appear at a level approximately one-third the distance from the larger to the smaller end of the egg. Pip holes then progressively develop until they reach about 0.7 cm in diameter about two days later in *C. psittacula* and *A. cristatella* and 0.5 cm in *A. pusilla* about three days after the initial cracking. With the egg tooth in contact with the shell the chick gradually cuts off the large end, pushes the resulting loose cap upwards, and emerges. The loose end is usually pulled back into "place" by a portion of adhering outer shell membrane. This sequence is similar in *F. corniculata* except that the pip hole, ultimately 0.9 cm in diameter, forms two to three days after the first cracks appear and the large end is cut off at an angle to the long axis of the egg rather than perpendicular to it as in the auklets.

These hatching methods are similar to that of *Cephus columba* (Drent, 1961) but the time involved in hatching by auklets is more variable than in *Alca torda* (Bédard, 1969), *C. columba* (Drent, op. cit.), and *Ptychoramphus aleutica* (Thoresen, 1964). In *F. arctica*, Myrberget (1962) found the average time from the appearance of the first cracks to emergence of the chick to be 4.3 days. In 37 out of 50 cases he found the "lid" of the egg inside the large section of the shell. Tuck (1961:155) stated that two or more days may be required for murre chicks (*Uria* spp.) to hatch, and occasionally "the adult assists by pecking away all or part of the hard, calcareous shell." Adult auklets were not observed in the present study helping chicks out of the eggs.

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GROWTH RATES AND SEX RATIOS OF RED-WINGED BLACKBIRD NESTLINGS

LARRY C. HOLCOMB AND GILBERT TWIEST

THE mean growth in weight and tarsus length for male and female Red-winged Blackbird (*Agelaius phoeniceus*) nestlings has been reported by Williams (1940). Holcomb and Twiest will report elsewhere on Redwing nestling mean growth and growth "rate." It was found that there was no difference in growth of Redwing nestlings raised either in a marsh or an upland habitat. There was some brood reduction, however, in the upland habitat. It is important to establish that Redwing nestlings grew at the same rate in upland and marshes because this paper reports growth of birds from both environments analyzed together.

Allen (1914), Beer and Tibbitts (1950), Meanley and Webb (1963), Nero (1956), and Orians (1961) have documented beyond any doubt that the Redwing is polygamous. A male usually has between one and three females in his territory; two is most common. This suggests an adult female-male ratio of 2:1. First-year males, however, do not usually breed, and since there is not adequate knowledge about the fraction of first-year females breeding, one cannot say that there are two adult females for every male.

In this paper the objectives are to 1) discover whether there is a difference in *growth rate* (as presented by Brody, 1945; Dawson and Evans, 1957, 1960; Banks, 1959; and Maher, 1964) in weight of male and female nestling Redwings, 2) show the mean growth and rate of growth in weight and body parts of male and female nestlings, 3) show the time of feather capsule projection and fringing and growth of feathers in eight major feather tracts of male and female nestlings, 4) show the growth of body parts, each of which contributes to ontogeny of behavior, and 5) evaluate methods of sexing nestling Redwings by weight, and to show some reasons why a difference may exist in the adult ratio of males and females.

METHODS AND PROCEDURES

The study was done at a marsh at Battle Creek, Michigan, in 1965 and in an upland region in Toledo, Ohio, in 1964 and 1965. The nests were visited at least once each day. With few exceptions, a nest was visited at 24 ± 1 hour intervals. Nestlings were marked in the sequence of hatching by placing fingernail polish on their claws (claw 1, 2, etc.). New polish was added as it became worn. The weight was obtained to the nearest one-tenth gram on a double-beam balance after the nestling had been handled sufficiently to cause voiding of wastes.

Measurements of growth were made on the following parts of nestlings:

toe span—distance from the tip of toe one to the tip of toe three when extended; nearest mm. This characteristic is important in the development of the righting reflex and allowing the nestling to grasp and balance (Holcomb, 1966).

total body length—distance from the anterior tip of the culmen to the tip of the tail (including rectrices when present)—nearest mm

tarsus—nearest one-half mm

wing—radiale region to the tip of the phalanges (before feathers were present) and to the tip of primary eight after it emerged (wing chord)—nearest mm

Three head portions were measured so that observers studying behavior of gaping as a parental stimulus could refer to more than one standard.

mandibular tomium—distance from the anterior tip of the lower mandible to the commissural point—nearest mm

mandible tip (culmen) to nostril opening—distance from the anterior tip of the culmen to the anterior edge of the nostril opening—nearest one-half mm

gape width—distance across the base of head from one commissural point to the other—nearest mm

Each of the eight feather tract regions were examined each day and if one feather capsule had pushed through the epidermis it was recorded as *projecting*. After the feather capsules had projected, they were examined each day, to determine when the capsule was broken and feather barbs were visible. This was called "fringing" of the feather capsule.

One feather was measured from each of eight tracts each day after projection occurred. In most tracts one could not be sure that the same feather was measured each day, but the feathers were so near the same length in an area that the choice of different feathers should affect the mean values very little.

The following feathers were measured to the nearest mm:

caudal tract—left outermost rectrix

alar tract—first (most proximal) primary (left wing)

humeral tract—the longest feather—(usually found in the middle of the tract running parallel with the body)

capital tract—center of the coronal region

spinal tract—longest feather in the interscapular region

ventral tract—longest feather in the axillar region

crural tract—longest feather in the mid-portion of the anterior side of the leg

femoral tract—longest feather in the mid-portion.

Wetherbee (1957) describes the regions from which feathers were measured in this study and Holcomb and Twiest will publish a report containing a figure showing the exact locations.

The mean and standard errors were calculated for all of the measurements. The *b* values (regression coefficients) for the slopes of the growth curves for weight were calculated and a two-sided Students' *t*-test was used for determining significance ($p < 0.05$).

Growth in Redwings over the entire nestling period was nonlogarithmic. Thus, in determining growth rate, the formula presented by Banks (op. cit.) was used.

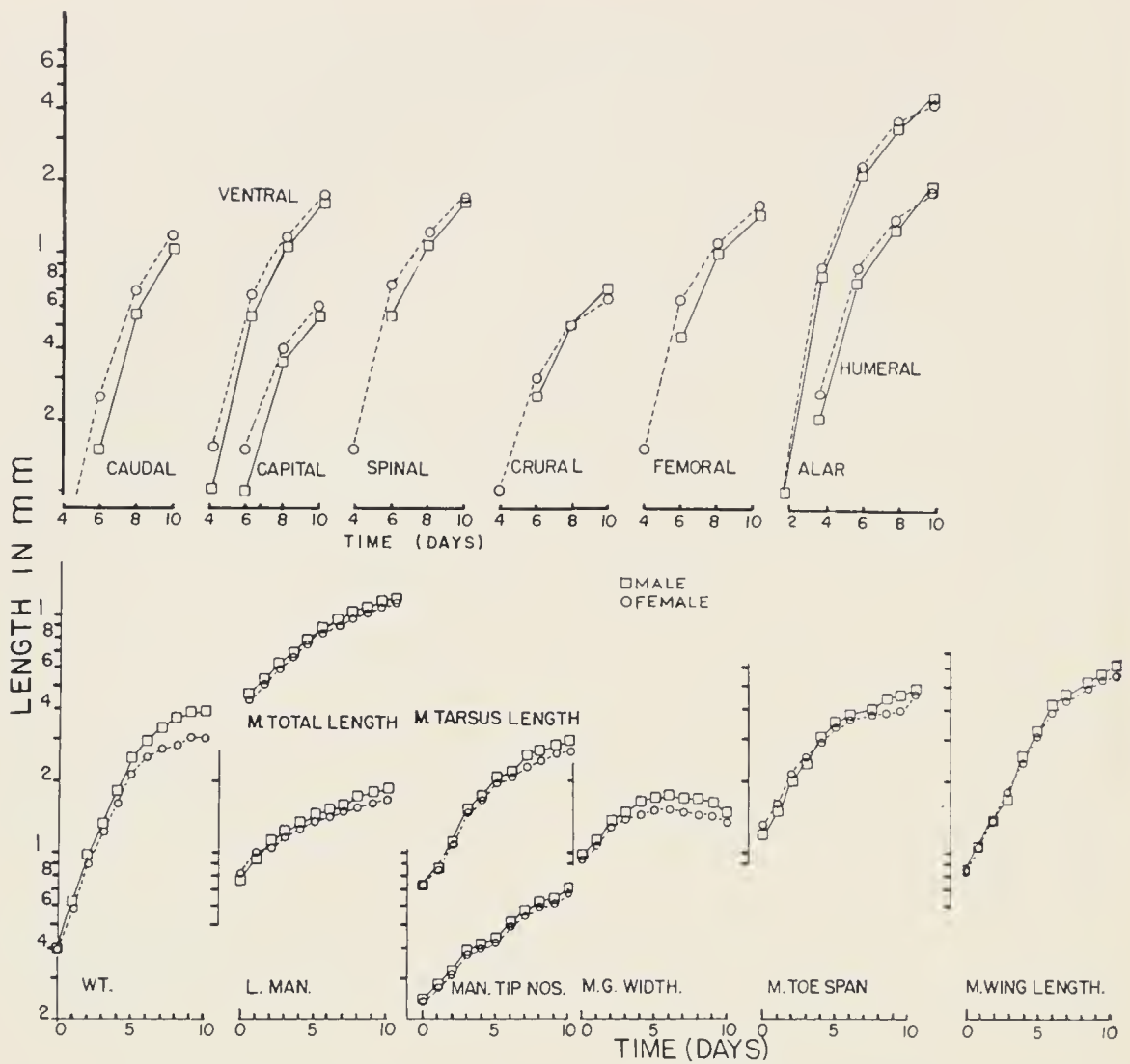


FIG. 1. Mean values are plotted in a semilogarithmic fashion for increase in weight (grams) and length (mm) of other body components and eight feather tracts of male and female Redwing nestlings. The smallest value is 0.5 mm; the greatest is 116.7 mm.

RESULTS AND DISCUSSION

Mean growth and growth rates.—Figure 1 shows the growth in weight of males and females on a semilogarithmic scale. There is a distinct separation of the growth curves for male and female nestlings and the slopes were significantly different.

Figure 1 shows the increase in weight and growth in length of different anatomical regions through day 10, and Table 1 shows the instantaneous relative growth rate (R). The mean growth increments are greater each day for male nestlings but not significantly different except for weight.

A simple index was calculated to show mean values of the rates of growth over the entire nestling period, i.e., the R (rate) values were summed for each characteristic and then divided by the number of days. The mean rate of

TABLE 1
REDWING MALE AND FEMALE NESTLING INSTANTANEOUS RELATIVE GROWTH RATES (R)
FOR WEIGHT AND OTHER CHARACTERISTICS

Day	Sex	N Wt.	R Weight	N Other char.	R Lower mandible	R Mandible tip to nostril	R Gape width	R Toe span	R Wing length	R Total length	R Tarsus length
0	M	47		34							
	F	58		36							
1	M	42	45	29	19	16	18	20	18	11	21
	F	61	43	37	18	16	18	22	20	13	22
2	M	43	46	30	18	15	19	26	27	15	25
	F	60	42	38	15	13	15	24	28	12	22
3	M	44	33	31	10	14	8	20	28	11	23
	F	61	34	36	12	16	9	22	31	13	25
4	M	42	34	29	10	12	6	23	37	13	22
	F	53	27	33	8	9	4	18	30	12	19
5	M	42	25	32	6	12	2	14	28	11	16
	F	58	24	36	7	13	1	13	28	9	16
6	M	46	18	34	5	9	2	8	21	7	12
	F	60	14	36	2	8	0.4	6	18	6	12
7	M	45	11	32	3	10	-2	5	13	7	10
	F	63	7	39	3	10	-1	4	13	6	5
8	M	41	7	28	4	8	-0.3	5	11	4	5
	F	56	4	38	2	7	-1	1	9	6	4
9	M	34	8	23	1	7	-2	2	8	6	2
	F	40	5	29	2	6	-1	3	7	6	2
10	M	22	2	18	3	3	-5	3	8	4	4
	F	20	1	17	1	4	-5	2	5	4	0.3
Index	M		23		8	11	5	13	20	9	14
	F		20		7	10	4	12	19	9	13

growth throughout the entire nestling period could then be compared for each component. Rates of growth were somewhat faster for males than females in most cases but there were no significant differences. Gape width was the only characteristic declining in size after day six. This was due to a decrease in the fleshy rictal portions. The index for growth over the 10-day nestling period indicates the relative growth of different portions of the body.

TABLE 2

PROJECTION AND FRINGING OF FEATHER TRACTS IN MALE AND FEMALE REDWING NESTLINGS
GIVEN IN PERCENTAGE OF INDIVIDUALS WHERE IT HAS OCCURRED

Day	Sex	N	Caudal		Capital		Spinal		Crural		Femoral	
			P	F	P	F	P	F	P	F	P	F
3	M	40			3		25		3		13	
	F	52			6		44		8		38	
4	M	38	11		8		95		76		95	
	F	48	42		27		98		85		100	
5	M	39	79		59		100		100		100	
	F	53	85		79		100		100			
6	M	38	100	3	100		21		18		29	
	F	53	100	6	100		49		42		51	
7	M	36		44		8		94		92		97
	F	53		49		32		98		92		94
8	M	32		100		100		100		100		100
	F	46		100		91		100		100		100
9	F	46				100						

Day	Sex	N	Alar		Humeral		Ventral	
			P	F	P	F	P	F
1	M	39		5				
	F	54		12				
2	M	40		93		3		
	F	55		95		9		
3	M	40		100		50		28
	F	52		100		62		48
4	M	38				100		95
	F	48				100		100
5	M	39		8				100
	F	53		19		8		15
6	M	38		87		68		71
	F	53		94		74		87
7	M	36		100		100		100
	F	53		100		100		100

Projection, fringing, and growth of feathers.—Table 2 shows the percentage of each sex that had feathers projecting from the epidermis and the capsules fringing on the ends. The females had feathers projecting and fringing somewhat earlier than males.

TABLE 3
REDWING MALE AND FEMALE FEATHER TRACT INSTANTANEOUS PERCENTAGE
GROWTH RATE (R)

Day	Sex	N	Caudal	Alar	Humeral	Capital	Ventral	Spinal	Crural	Femoral
3	M	28		115						
	F	32		126						
4	M	26		100	124					
	F	33		87	106		119	127		146
5	M	30		57	82		99	103	76	84
	F	36	97	52	77		84	82	78	83
6	M	27	78	41	51	95	61	64	60	64
	F	34	82	37	45	84	55	61	54	54
7	M	24	69	24	32	59	38	41	25	44
	F	33	69	24	31	56	40	33	35	37
8	M	20	46	21	25	47	29	30	33	29
	F	28	40	16	17	29	22	25	11	17
9	M	16	39	15	22	27	25	20	16	25
	F	23	35	15	20	24	22	18	21	20
10	M	12	26	11	16	20	22	23	24	18
	F	13	21	7	9	11	14	13	7	15
Index (for first five days)	M		52	67	63	50	50	52	42	49
	F		64	65	55	41	64	66	40	67

Figure 1 shows the mean growth of feathers and Table 3 shows the rate of growth in the different feather tracts. Males and females had feathers of about the same length at fledging. An index was obtained by calculating the mean of the growth rate for only the first five days of growth for each feather tract because the caudal and capital tracts did not appear as early as the other feather tracts and comparative values were desired.

The feathers grew at a faster rate than other characteristics measured. This is necessary if they are to provide their function by the time fledging occurs.

Sexing nestlings by weight.—The sex was determined by weight after nestlings reached an age of eight to ten days. Males had an overall different appearance. Their feather cover developed slower than females and they were more clumsy in their movements. Each individual was marked so that weight increases could be traced backward in time. The values for weights of nestlings are shown in Figure 2. There is overlap in weights of males and females yet on day 10. On day seven, 24 of 64 females weighed 27 or more grams and

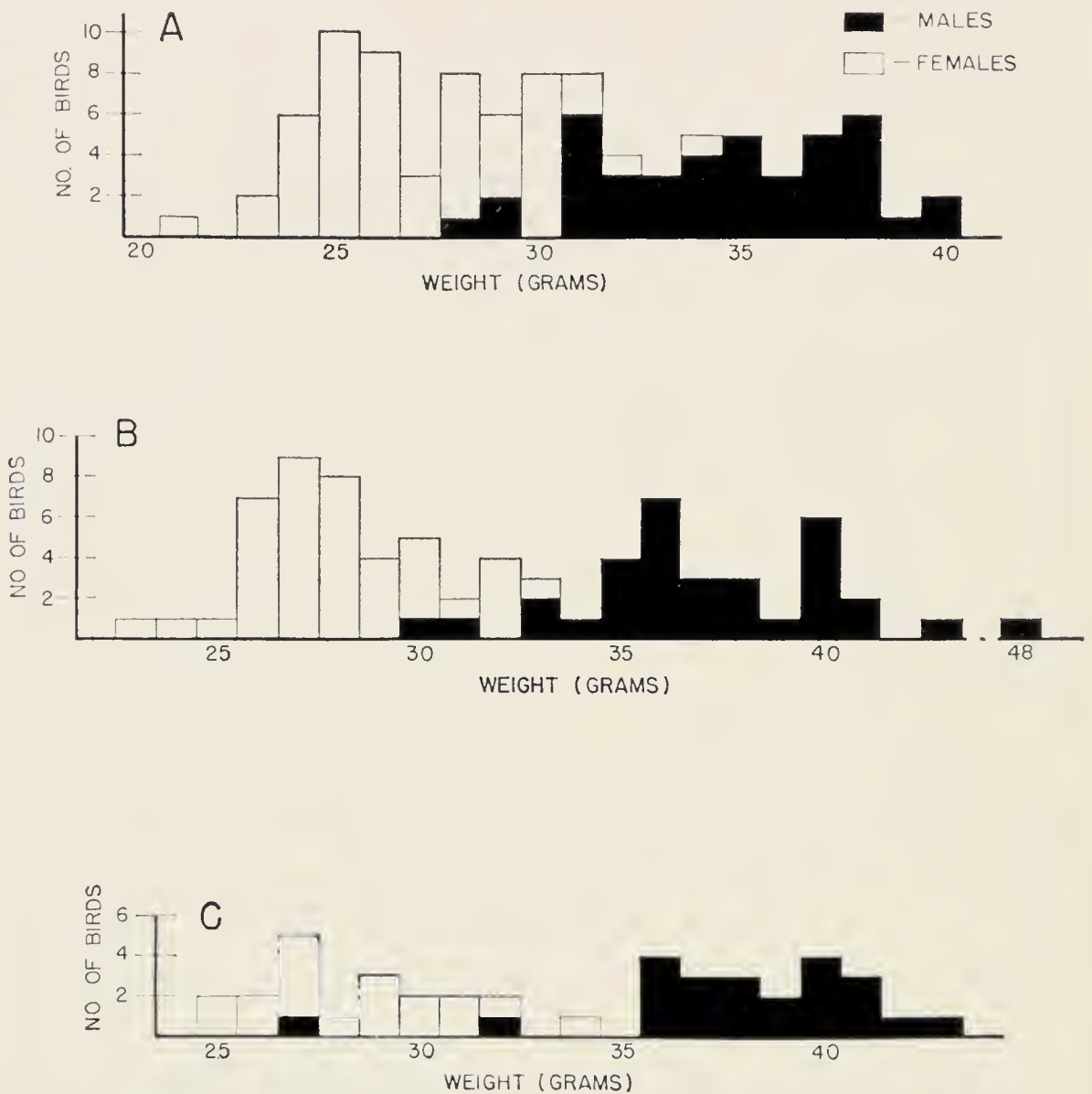


FIG. 2. Weights of Redwing male and female nestlings on A) day 8; 95 birds, B) day 9; 75 birds, C) day 10; 41 birds.

two of 45 males weighed less than 27 grams. Nero (1961) reported that Redwing nestlings could be sexed on the basis of weights beginning on day seven: 7th day—female below 27 g, male above; 8th day—female below 30 g, male above; 9th and 10th days—female below 33 g, male above 36. Williams (1940) reported too much overlap yet on day seven. His method on day eight was the same as Nero's. Williams' data for day nine indicate all females are 33 grams or below and all males 37 grams or above, and for day 10, females 33 or below and males 38 or above. If we used either of the methods proposed by Nero or Williams to sex our nestlings, we would have made several errors. We concede that it would be impossible to show a method that would work

without failure in sexing Redwing nestlings. We would prefer not to recommend criteria for determining sex before day eight. Even then, there will be some error when using only weight. We would prefer to make these recommendations for sexing nestlings of known age: Day 8—female under 31 grams, male 31 grams or over; Day 9—female under 33 grams, male 33 grams or over; Day 10—female under 33 grams, male 35 grams or over.

Ratio of males to females fledged.—The egg sequence producing males and females was: egg one—16 males, 24 females; egg two—20 males, 19 females; egg three—11 males, 15 females; egg four—4 males, 10 females. The sex was determined for 50 males and 68 females. Of this group, 41 males (82 per cent) and 54 females (79 per cent) were successfully fledged.

The mean duration of nestling life is shorter for females than males (9.2 vs. 9.7 days). The reasons for earlier fledging in females may well be that they obtain the adult size faster. The feathers project and fringe a little earlier in females and by day nine they are as long or longer than males in every tract. There is also faster feather development compared to total body weight. For instance, the first primary (alar tract) has the same mean length for males and females on day nine. On day nine, males weigh a mean of 9.2 more grams than females, and the length of the wing is only 3.2 mm longer. This would suggest that the females leave earlier, because they have lighter wing loading than males.

We believe that there may be no difference in the ratio of males to females in the first summer, and if there is any difference, it may favor females. Males stay in the nest somewhat longer than females. As young are more subject to predation than eggs (Young, 1963), more females may be fledged. The capture of more males than females in mist nets (Meanley, 1964) and live traps (Giltz, pers. comm., and trapping by Holcomb) may result from males being attracted to other birds in a trap, due to aggressive or gregarious tendencies. Perhaps males respond faster to calls of individuals already captured. The more aggressive nature of males may also make them less timid than females in approaching a capturing device. This same lack of timidity may also make them more vulnerable to predation than the females, and thus contribute to an excess of females for a polygamous mating system (see Selander, 1965).

SUMMARY

The *b* values for the slope of the growth curves for weight of Red-winged Blackbird male and female nestlings showed a significant difference ($p < 0.05$); the males grew faster.

An index for rates of growth for weight, lower mandible, mandible tip to nostril, gape width, toe span, wing length, total length, and tarsus length showed that males grow faster only in weight. Growth rates are presented for eight major feather tracts of males and females; there were no sexual differences.

Feather capsules project from the epidermis and fringe on the ends in a greater percentage of females earlier than males. Therefore, although feathers grow at a little faster rate in males, females have feathers nearly the same length in each tract near fledging time.

Red-winged Blackbird nestlings can usually be sexed on the basis of weight by day eight. However, there was some overlap in weights of male and female nestlings on day 10. A revision of a method for sexing nestlings on the basis of weight is given.

A ratio of males to females hatched from eggs of known laying sequence is given. The sex was determined on 50 males and 68 females of which 41 males and 54 females fledged. A *secondary ratio* of 50:50 is suggested and hypotheses for reasons leading to an adult ratio in favor of females are given.

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16214. 14 FEBRUARY 1968.

REQUESTS FOR INFORMATION

Desire data on body and/or feather weights in California quail and ring-necked pheasant for Ph.D. research topic. Especially desire data from limited circulation or unpublished sources. Can also utilize similar data on other phasianid species. If possible, please list individually with date, location, sex of bird, age of bird if determinable and name of collector. Send to Carl Phillips, Dept. of Zoology, U.B.C., Vancouver 8, B.C., Canada.

During the autumn migration of 1970 the Ontario Bird Band Association hopes to band and color-mark several hundred Semipalmated Sandpipers and Sanderling at Long Point, Ontario. Information on the movement of these sandpipers is essential to research presently underway on the energy requirements of their migration. We would greatly appreciate it if anyone sighting these birds would report their observations to Dr. A. Salvadori, Department of Mathematics and Statistics, University of Guelph, Guelph, Ontario.

The following information would be appreciated; Species: Location: (including nearest city or town) Dates: Color: (birds will be colored on the breast or abdomen with a single color, either pink, orange, blue, green, yellow or purple). Leg that has been banded: (This will tell if the bird is an adult or an immature.)

Any information on what other birds are with the marked individuals would be very useful.

COWBIRD PARASITISM AND NESTING SUCCESS OF LARK SPARROWS IN SOUTHERN OKLAHOMA

GEORGE A. NEWMAN

FRIEDMANN (1963) considers the Lark Sparrow (*Chondestes grammacus*) to be a relatively uncommon host of the Brown-headed Cowbird (*Molothrus ater*). During the summer of 1968, I made observations of 33 active Lark Sparrow nests in the vicinity of the University of Oklahoma Biological Station on the north side of Lake Texoma approximately 2 miles east of Willis, Marshall County, Oklahoma. These observations were made from 7 June 1968, through 1 August 1968. The purpose of the study was to seek information on the incidence of Cowbird parasitism upon Lark Sparrows and to gain additional nesting data on Lark Sparrows. Dr. George M. Sutton and I banded a total of 35 Lark Sparrow nestlings during the time of the study.

NESTING SITES

Of the 33 nests observed, 10 were located on the ground in pasture land which was grazed periodically throughout the summer. Another ground nest was located in a cultivated peanut field. These nests were usually placed at the bases of small herbaceous or woody plants which provided some shade during the day. Three of the ground nests, however, were built in short grasses and were relatively unprotected. The following eight species of plants were utilized as ground nesting sites: *Asclepias viridis*, *Cnidocolus texanus*, *Trifolium repens*, *Diospyros virginiana*, *Cynodon dactylon*, *Andropogon scoparius*, *Smilax Bona-nox*, and *Arachis hypogaea*.

Twelve species of plants were used as nesting sites by Lark Sparrows that built their nests above ground (Fig. 1): *Cupressus arizonica*, *Pinus* sp., *Juniperus virginiana*, *Rosa setigera*, *Lagerstroemia indica*, *Thuja occidentalis*, *Ulma alata*, *Salix nigra*, *Quercus stellata*, *Yucca* sp., *Crataegus* sp., *Maclura pomifera*.

Three nests were unusual and warrant mentioning. Nest 23 was situated in a cavity of a dead willow (*Salix nigra*). The nest was loosely constructed and consisted of a matting of medium sized grasses upon which a lining of small grasses and rootlets was placed. When found this nest had six eggs, four Lark Sparrow eggs and two Cowbird eggs (Fig. 2). The nest was destroyed by a predator before the eggs hatched. Nest 6 was built under a "cow chip" which had been raised by grass. The "chip" completely surrounded the nest except for an opening to the southeast. Four Lark Sparrow eggs were laid in the nest; all of them hatched. A heavy rain washed away the nest before the young fledged. The foundation of nest 25 was built by a Mockingbird and the lining



FIG. 1. Lark Sparrow on nest in *Juniperus virginiana*.

placed by a Lark Sparrow. I did not observe any encounters between the two species. It appeared that the Mockingbird had abandoned the nest before its completion and only after it was abandoned did the Lark Sparrow utilize it. Two Lark Sparrow eggs were laid in the nest; both eggs hatched and the young fledged.

PREDATION

Nesting success was significantly greater for nests built above ground (44.5 per cent) than for nests built on the ground (23.7 per cent). These percentages are based upon the number of Lark Sparrows fledged per total Lark Sparrows eggs laid. The greater success of nests built above ground is probably because these are better protected from the elements and from predation.



FIG. 2. Nest 23 showing four Lark Sparrow eggs and two cowbird eggs.

TABLE 1
SUCCESS OF PARASITIZED AND NON-PARASITIZED NESTS

Nest	Height (Meters)	Cowbird Eggs	Parasitized			Non-parasitized	
			Cowbirds Fledged	Host Eggs	Hosts Fledged	Eggs	Fledged
1	ground	1	0	3	0		
2	ground	1	0	3	0		
3	ground	1	0	3	0		
4	ground					3	0
5	ground	1	1	3	3		
6	ground					4	0
7	ground	1	0	4	0		
8	ground	1	0	4	0		
9	1.22					4	3
10	1.83					4	3
11	1.22	1	1	3	3		
12	ground					4	4
13	0.74					4	0
14	ground					4	0
15	1.02					4	3
16	1.81					4	4
17	3.66					4	0
18	4.58	1	1	3	1		
19	3.96	2	0	3	0		
20	1.94					4	4
21	1.52	2	0	4	0		
22	ground	1	0	3	2		
23	2.44	2	0	4	0		
24	6.10	2	0	3	0		
25	1.52					2	2
26	5.04					4	3
27	1.52					3	0
28	1.52					2	2
29	1.22	1	0	2	0		
30	1.22					4	4
31	0.92					3	?
32	1.22					4	0
33	2.14	1	?	1	?		
Totals		19	3	46	9	65	32

Though I had no direct evidence of predation by snakes, populations of black rat snakes (*Elaphe obsoleta*) and blue racers (*Coluber constrictor*) were known to be high in the study area during the time of the study. Of the nests under observation, 38.7 per cent were preyed upon and 16.1 per cent were abandoned

for causes other than predation. Four of the nests which were preyed upon were disrupted, indicating predation by mammals. Eight other nests were not disrupted, indicating that snakes may have been responsible for the predation.

COWBIRD PARASITISM

Fifteen of 33 (45.5 per cent) nests were parasitized by the Brown-headed Cowbird (Table 1). Wiens (1963) reported an incidence of 19.0 per cent of cowbird parasitism upon Lark Sparrows in the southern Oklahoma region for the years 1956, 1960, and 1961, based on a total of 21 nests. Of 30 incidences of parasitism reported by Friedmann, only two are known to have successfully fledged young cowbirds. Three out of 14 nests in this study are known to have fledged cowbirds. Of 18 cowbird eggs laid, 33.4 per cent hatched and only 15.8 per cent of the young were successful in leaving the nest. Forty-five host eggs were laid in the same 14 parasitized nests; 17 (37.8 per cent) eggs hatched and 9 (20.0 per cent) young fledged.

A total of 58 eggs were laid in 16 non-parasitized nests; 42 (72.4 per cent) of these eggs hatched and 32 (55.2 per cent) young successfully left the nest.

This cowbird parasitism was substantially greater among Lark Sparrows than had been previously recorded. The absence of the Bell's Vireo (*Vireo bellii*), a common host species of the cowbird (Sutton, 1967), might have caused a shift in parasitism to a less frequent host species, i.e. the Lark Sparrow. Bell's Vireo has in the past been a relatively common species of the study area.

Of 11 ground nests, 7 (63.6 per cent) were parasitized, whereas, 8 out of 22 (36.4 per cent) of the "above ground" nests were parasitized. The ground nests on pasture land were probably more easily accessible to cowbirds than those nests built in trees and shrubs, and there were larger numbers of cowbirds in the pasture land than there were in the other nesting areas.

Egg-laying by Lark Sparrows was at its greatest peak during the second week in June (Fig. 3). Cowbirds laid their greatest numbers of eggs during the first two weeks of June and the first week of July. The latest date for a cowbird egg being laid during this study was 5 July. Sutton (1967) records the latest date for egg laying by cowbirds in Marshall County as 3 July. During the second week of July, after cowbird egg-laying had ceased, egg-laying by Lark Sparrows reached another peak.

Baepler (1968) states that good evidence for double-broodedness in the Lark Sparrow is lacking and it is his conclusion that double-broodedness probably does not occur in this species. On 26 June I observed an adult Lark Sparrow feed a young Lark Sparrow on a telephone wire. This same adult was actively building nest 22 between feedings of the young bird. Although this is not

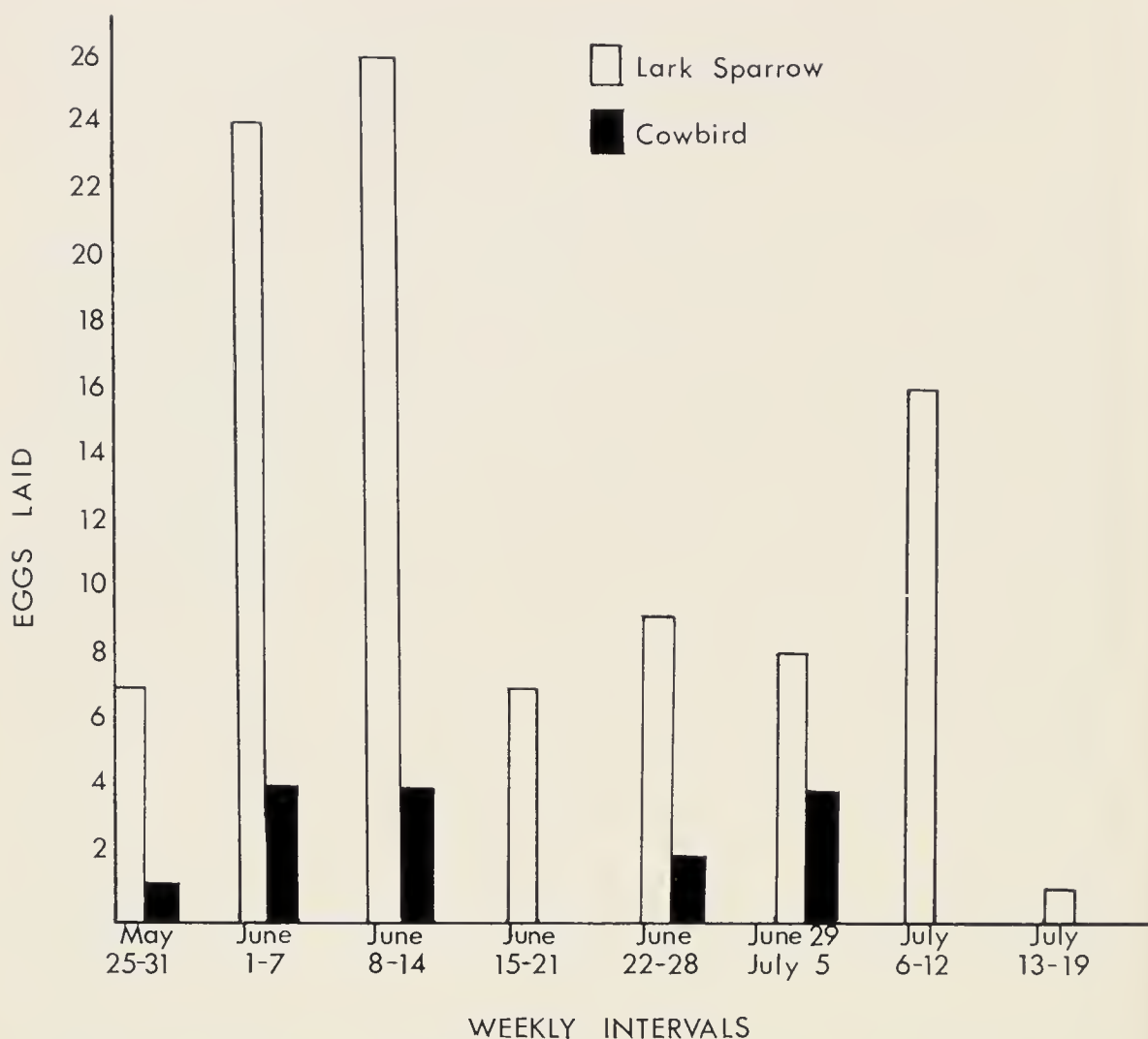


FIG. 3. Number of eggs laid by Lark Sparrows and Cowbirds in weekly intervals from 25 May 1968, to 19 July 1968.

definite proof of a second brood, it is evidence in favor of two broods being raised by the same Lark Sparrow. This points out the need for careful investigations using color-banded birds to clear up the question of double-broodedness in this species. Evidence presented in this paper does indicate that late broods, whether they be second broods or second attempts, do encounter little or no parasitism by the Brown-headed Cowbird.

SUMMARY

Data were collected on 33 active Lark Sparrow nests from 7 June 1968, to 1 August 1968 in the vicinity of the University of Oklahoma Biological Station. Parasitism of Lark Sparrows was greater than had previously been reported. A comparison of the success of parasitized versus non-parasitized nests is presented. Egg laying dates for Lark Sparrows and Cowbirds are presented and analyzed.

General nesting site data is presented along with a detailed description of three unusual nest sites. Notes on predation are also given.

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I am grateful to Dr. George M. Sutton for his guidance and encouragement during this study. I would also like to thank Dr. Carl D. Riggs, Director of the University of Oklahoma Biological Station, and Assistant Director Dr. Loren G. Hill for granting me the opportunity to assist at the biological station during the summer of 1968. Mr. Freeman Thomas gave valuable assistance to me in the identification of plants.

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23 OCTOBER 1968.

ANNOUNCEMENT

A collaborative program to study the migration of the Whistling Swan involving The Johns Hopkins University, the Canadian Wildlife Service, the U.S. Fish & Wildlife Service, the U.S. Air Force, and State and Provincial game agencies has been organized. Swans have been marked with colored bands, colored collars, and dyed feathers. Persons who saw marked swans last spring, or who see them this fall should report the details to: Dr. William J. L. Sladen, Johns Hopkins University, 615 N. Wolfe St., Baltimore, Maryland 21205. Those persons who are so located as to see large numbers of swans in migration might well contact Dr. Sladen for report forms and details about the color marking scheme.

DUST-BATHING SITES SELECTED BY RUFFED GROUSE

DALE HEIN

AN opportunity to study the preferences of Ruffed Grouse (*Bonasa umbellus*) for dust-bathing sites occurred near Highlands, Macon County, North Carolina. During June 1968, grouse commonly dust bathed along an abandoned logging road which wound northeastward for 2.5 km from Wildcat Cliffs. The straight-line distance traversed was 1.4 km.

The trail exposed many possible dusting substrates—litter and duff areas, decaying logs and stumps, silty sediments, clay banks, gravelly areas where intermittent watercourses crossed the trail, and numerous bare soils obviously different in texture, structure, and color. The hilly topography and the winding trail also presented variations in site factors in addition to substrate types.

The trail provided virtually the only opening in dense second growth, mesic vegetation in various intermediate stages of succession (Fig. 1). Important species of the discontinuous canopy included red maple (*Acer rubrum*), cherry birch (*Betula lenta*), tulip poplar (*Liriodendron tulipifera*), and white pine (*Pinus strobus*). The dense understory was characterized by thickets of great rhododendron (*Rhododendron maximum*) interspersed with less abundant species such as flowering dogwood (*Cornus florida*). In many places the old road was reduced to a narrow trail winding through brambles (*Rubus* sp.). Ferns and herbs such as galax (*Galax aphylla*) covered much of the ground away from the trail. Mean elevation of the study area is 1200 m. Annual precipitation averages 200 cm, and the mean June temperature is 19°C. Odum (1950) gave a succinct description of the avifauna and plant communities of the Highlands Plateau, which includes this study area.

In a monumental study of Ruffed Grouse in New York, Bump et al. (1947: 271) found that dust baths were located in any spot offering suitable material and receiving the sun's rays during some portion of the day. The material utilized was varied, the primary requirement being looseness and dryness. Dry, rotten wood of old stumps and logs was most frequently used with fine, dry earth a close second. In northern New York fine sand was commonly favored. Dust bathing by Ruffed Grouse is generally believed to be a maintenance activity for feather care and riddance of ectoparasites (Edminster, 1954:204; Forbush and May, 1955:137).

METHODS

Two grouse were flushed from dust bathing sites when I first walked the trail during midafternoon on 1 June. Two grouse were flushed from different dusting sites on 6 June, and locations and general site characteristics were noted for 20 dusting scrapes, some ap-



FIG. 1. Typical dust-bathing site of Ruffed Grouse near Highlands, North Carolina, June 1968. A fresh dusting scrape is located in front of the binoculars.

parently older and used more than others. Grouse scrapes were easily identified by their size and often by presence of grouse feathers and droppings. There was no evidence of dust bathing by any other species larger than the Brown Thrasher (*Toxostoma rufum*). Existing scrapes were obliterated by more than 9 cm of rain on 8 June. Cloudy, humid weather and light rains on 9 and 12 June kept the soil surfaces damp and no dusting scrapes were found along the trail on 12 June. However, 13 and 14 June were warm and sunny with low humidity. I anticipated that most grouse would use the newly dried soils on the afternoon of 14 June, after a week without dusting, and 14 new scrapes were found and examined in detail on 15 June during 09:00–13:00.

Aspect, exposure, adjacent vegetation, and distance to closest dusting scrape was noted for each of the 14 scrapes. Maximum depth and rim-to-rim distances of longest and shortest axes were measured. At each scrape 200 cc of substrate was collected from the rim and surface of the dusting depression. Each of the 14 samples was oven-dried, weighed, and shaken for 30 minutes through six sieves in the U. S. Standard Sieve Series, after which each separate was weighed. The seven separates approximated the classification of soil particles established by the Department of Agriculture (Lyon et al., 1952:46), except the silt and clay separates were combined. Bulk density, particle density, and color were also recorded for each sample.

A large rock was placed in each scrape after the substrate sample was collected. The trail was checked for new scrapes on 16 June, and a final check of new and old scrapes was made on 22 June.

TABLE 1
TEXTURES OF SOIL USED BY RUFFED GROUSE FOR DUST BATHING NEAR HIGHLANDS,
NORTH CAROLINA, 15 JUNE 1968

Sample	Percent of sample in each soil separate						
	Gravel	Very coarse sand	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt and clay
Coarsest of 14	8	18	30	25	12	4	3
Average of 14	6	9	24	29	19	8	5
Finest of 14	3	8	21	27	21	12	8

RESULTS

The dimensions and locations of the 14 dusting scrapes were similar. The average size of the scrapes was $30 \times 25 \times 3.2$ cm. Extreme rim-to-rim distances were 45 and 18 cm, and depths ranged from 1 to 5 cm. In three cases, the distance between scrapes was less than 2 m; all other intervals were more than 40 m. Five scrapes were overhung by brambles, and all others were less than 2 m from thick cover. Four scrapes were in relatively straight sections of the trail, while 10 were on the outside (greater) curve of a bend in the old road. Two sites had an east aspect, and 12 had west or southwest aspects with less than 15° slope.

Textures of soils in the dusting scrapes were remarkably similar. Approximately 90 per cent of each sample was comprised of various classes of sands (Table 1). The coarsest sample contained 8 per cent gravel (particles greater than 2 mm in diameter), and the finest sample contained 8 per cent silt-clay (particles less than 0.05 mm diameter).

The bulk densities of the 14 samples averaged 1.2, and the particle density averaged 2.6. Both figures were in the lower range of normal values for sandy soils (Lyon et al., 1952:56-59). Bulk densities would have been higher in undisturbed areas adjacent to the dusting scrapes.

Soil colors were compared with Chapman's (1914:26-27) color chart. Closest matches for the 14 samples were 5 ochraceous buff, 3 brownish gray, 3 ashy, and 1 each grayish brown, brownish ashy, and pearl gray. Colors in the chart of Palmer (1962:4-5) did not match soil colors as well; smoke gray, buffy brown, and cinnamon were chart colors resembling the soil colors.

Approximately 24 hours after the collection of the soil samples and the placing of a large rock in each scrape, the trail was rechecked, and seven new scrapes were found. Three were within 2 m of an old scrape, and four were 8, 20, 20 and 70 m from an old scrape. All were at sites similar to those sam-

pled. When the trail was last checked 6 days later, 11 grouse dusting scrapes were identified excluding the 14 sampled and destroyed earlier. All were similar in appearance and location to those described earlier.

DISCUSSION

Four factors were evidently important in determining location of dust bathing sites: (1) sand substrate, (2) exposure to the sun, (3) proximity of dense cover, and (4) maximum visibility for the grouse of clear routes of approach to the site. Thus, the typical scrape was on the north and outside of a curve in the trail, which provided the best view in both directions. The site was overhung by brambles or adjacent to similar escape cover. The substrate was sand, and the site sloped slightly providing a south aspect. Obviously these factors maximized protection from predators while dust bathing and provided dry, loose dusting material. In this area of high rainfall and frequent heavy dew, many substrates, such as rotting logs and litter, were seldom dry enough for dusting material.

Soil colors at dusting sites were generally similar to colors predominating in Chapman's (1914:273) description of Ruffed Grouse. One-third of the samples were ochraceous buff, the color Chapman used to describe throat, breast, and some variegating of the back. However, the data were insufficient to persuasively indicate that grouse selected dusting material of certain colors.

Although the sample of sites reported here is small, they were remarkably uniform. During June cursory examination of more than 20 other grouse dusting sites in other parts of the Highlands Plateau agreed with the detailed examination of 14 sites described.

Some unanswered questions include (1) what determines frequency of dust bathing by an individual bird, (2) does more than one bird use the same scrape, and (3) how important are suitable dusting sites in the habitat requirements of the species?

SUMMARY

Site factors and soil characters associated with dust bath locations of Ruffed Grouse were investigated near Highlands, North Carolina. Important factors were those which combined to provide dry, loose substrate and safety from predators.

ACKNOWLEDGMENTS

This research was aided by the National Science Foundation grant-in-aid, NSF GB 2496, made to the Highlands Biological Station and administered by Dr. Thelma Howell, Executive Director of the station.

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DEPARTMENT OF FISHERY AND WILDLIFE BIOLOGY, COLORADO STATE UNIVERSITY,
FORT COLLINS, COLORADO 80521, 3 JANUARY 1969.

PUBLICATION NOTES AND NOTICES

BIRDS OF ASIA. Illustrations from the lithographs of John Gould. Text by Abram Rutgers. Taplinger Publishing Company, New York, 1969: 7¼ × 9⅞ in., 321 pp., 160 col. pls. \$15.00.

This is the third in the series, after "Birds of Europe" (1966) and "Bird of Australia" (1967), reproducing the lithographs of Gould with text by Rutgers. Comments made in the review of the first book (see *Wilson Bull.*, 79:255-256, 1967) and in the notice of the second (*Wilson Bull.*, 80:247) are applicable to this volume which is practically identical in format and presentation.—O.S.P.

HISTOIRE NATURELLE DU GODE, *Alca torda*, L., DANS LE GOLFE SAINT-LAURENT, PROVINCE DE QUÉBEC, CANADA. Par Jean Bédard. Étude du Service Canadien de la Faune No. 7, Ministère des Affaires Indiennes et du Nord Canadien, Ottawa, 1969: 79 pp., 40 figs., 11 tables. \$1.25.

An English edition of this extensive study of the Razorbill is scheduled for publication in 1970.

CATALOGUS FAUNAE GRAECIAE. Pars 2, Aves. By W. Bauer, O. v. Helversen, M. Hodge, and J. Martens. Privately published, 1969: 203 pp., 2 maps. \$4.75. (Copies may be purchased from Max E. Hodge, 6345 Western Avenue, Washington, D.C.)

In German. A more comprehensive "Birds of Greece," to be published in English, is in preparation.

LAS AVES DE TIKAL. By Frank B. Smithe. Litografia Byron Zadik y Cia., Guatemala, C.A., 1969. Soft Cover Edition: \$3. (Obtainable from the Asociacion Tikal, Avenida de las Americas 6-19, Zona 14, Guatemala City, Guatemala, C.A.)

A Spanish language edition of Smithe's "Birds of Tikal," 1966 (for review see *Land, Wilson Bull.* 80:244-246, 1968). All profits from the sale of this edition go to the Asociacion Tikal, a non-profit organization which supports local interest in conservation and archaeology in Guatemala.

OBSERVATIONS ON THE BREEDING BIOLOGY OF THE VERMILION FLYCATCHER IN ARIZONA

WALTER KINGSLEY TAYLOR AND HUGH HANSON

DURING the period 6 April to 2 June 1967 we made observations on three nesting pairs of Vermilion Flycatchers (*Pyrocephalus rubinus*), two of which had second broods. Two additional pairs were in the area as well as a territory holding male, of much lighter coloration, that was believed to have never mated. None of the flycatchers were marked for individual identification.

Our observations were made in a well-developed mesquite (*Prosopis juliflora*) floodplain woodland locally known as Coon's Bluff Recreational Area, in Tonto National Forest, approximately 16 miles northeast of Mesa, Maricopa County, Arizona. Typical Lower Sonoran desert vegetation occupies adjacent upland regions.

HOSTILE BEHAVIOR

A few instances of prolonged conflict and aggressiveness between two flycatchers were observed. On 8 April at 07:30 the male of pair one and the light-colored unmated male chased each other for approximately 10 minutes. The mated male, evidently defending his territory, was the more aggressive individual. He made several short pursuit flights at the unmated male who invariably retreated. At the termination of each chase, the two males perched 10 to 20 feet apart. Their crown feathers were erect. The tail was spread, hanging downward, and was frequently flicked. Each emitted a loud, sharp *peent* note (see below). Occasional loud bill snapping sounds were produced, but the Gape Display mentioned by Smith (1967) was not seen. Evidently, the light-colored male was both the intruder and loser.

Once a male flycatcher terminated a flight display to chase a Violet-green Swallow (*Tachycineta thalassina*) in flight nearby. Lucy's Warbler (*Vermivora luciae*) was driven from the nest site by both sexes on three occasions. Once a male flycatcher chased a female Audubon's Warbler (*Dendroica auduboni*) from the nest tree. Brandt (1951) cited an incident of a male flycatcher attacking a male House Finch (*Carpodacus mexicanus*), but we found a pair of House Finches and flycatchers nesting in the same mesquite. On another occasion, however, the male flycatcher of a different pair chased a singing male finch from a nest with nestling flycatchers.

VOICE

Four distinct vocalizations were recognized. The primary functional significance of each is believed to be understood.

Song—The song is produced repeatedly by the male during the elaborate display flight. The song sounds like the words *pur-reet* with the first portion consisting of rapid repeated rolling notes. On infrequent occasions, perched males gave the same or at least portions of a similar song throughout the day. The song is produced by mated and unmated males.

Peent note—This is the typical call of the species and is commonly produced by both sexes. Each *peent* note is sharp sounding and loudly or softly given, depending upon the circumstances. It was produced by disputing males and by both sexes during displacement activities. In these circumstances, the individual notes were loud. The male used this call when he arrived to feed the incubating or brooding female. In these instances, the individual notes were not nearly as loud as during the disputes.

Feeding notes—These notes sounded as softly, quickly produced *piks* given by adults when feeding nestlings and probably alert the nestlings of the parent's presence.

Nestling notes—These peeping sounds were produced by disturbed nestlings. They were given at a rapid rate and are quite loud from the first day of hatching.

NESTING BIOLOGY

Nest building—The female built the nest but the male on several occasions accompanied her to the building site. A nest was found under construction on 6 April. Two days later the female was actively building on the structure. In another nest located 8 April shortly after construction had begun, an additional four days elapsed before the first egg was laid. Newly-constructed nests were used in the two cases of second nestings. Materials from one of the first nest were used in building the second structure.

Clutch size and egg-laying—Four clutches of three eggs and one of two eggs were observed. In two nests, the eggs were not laid on consecutive days.

Incubation period—Bent (1942) stated the incubation period as about 12 days and Wheelock (1904) gave 12.5 days required for the incubation of three eggs. In three nests we observed the incubation period (elapsed time between laying of the last egg to hatching of that egg) was 14 to 15 days. The clutches were incubated during late April.

Incubation behavior—Incubation was performed by the female, but, the male of one pair on two occasions entered the nest for less than one minute. Once the female chased the male away shortly after he entered the nest. In both instances, the male definitely did not remain in the nest long enough to incubate nor could we see any evidence of an incubation patch on the male. The presence of this structure could easily be detected on the female. Bendire (see Bent, 1942) stated that "the male assists [in incubation] to some extent,

as I have on two occasions seen one sitting on the eggs." Possibly his observations are comparable to our observations described above.

In two pairs the female spent an appreciable amount of time on the nest before the clutch was completed. The length of time on the nest during these periods was typically short, but frequent. Davis, Fidler, and Davis (1963) found that the female Western Flycatcher (*Empidonax difficilis*) spent considerable time on the nest before the clutch was completed.

During incubation and brooding, the males of pairs one and three brought food to the incubating female on the nest. This behavior never occurred in pair two during 210 minutes of observations spaced throughout incubation. The male of pair two, however, like the other males, fed the female off the nest. Feeding of the female by the male occurred with a slightly higher frequency on than off the nest. The male usually perched a short distance from the nest when he came to feed the female. He then gave *peent* notes which obviously announced his presence; he would spread his tail as it hung down and suddenly fly to the female. The male quickly deposited the food into the female's mouth and flew away. Sometimes the female gave subdued *peent* notes when the male appeared with food. She usually remained on the nest after these feedings; occasionally she left with the male. At times, the male did not go to the nest and the female flew to him and took the food. Copulation was frequently observed after these feedings. Twice the male with food flew straight to the nest while the female was absent. On both occasions, the female suddenly appeared and flew to the male at the nest. Both birds fluttered about as the male fed the female. After these feedings, they flew from the nest. The female never begged for food during any of these feedings.

The female often brought nesting materials when returning to incubate. She typically went to and from the nest alone, silently, and in a direct manner. She frequently terminated attentive periods to pursue nearby flying insects. The female's time spent off the nest was devoted to hawking insects near the nesting area.

In 424 minutes observing pair three, with nestlings 1 and 3 days old, the female had 43 attentive periods ranging from 20 seconds to 17.5 minutes. The mean time spent on the nest was 6.4 minutes and the percentage of attentiveness was 63. The mean inattentiveness through a total of 38 inattentive periods for this female was 4.8 minutes and ranged 20 seconds to 15 minutes. During 110 minutes observing another nest with one nestling that hatched that morning, the female had eight attentive periods ranging from 1 to 26 minutes. The mean time spent on the nest was 11 minutes and the percentage of attentiveness was 30. The mean inattentiveness through a total of seven inattentive periods for this same female was 3.1 and ranged 1 to 6 minutes. One incubat-

ing female remained on the nest for 39 consecutive minutes. This was the longest period any incubating or brooding female spent on the nest. The male did not feed the female during the 39-minute period.

The female of pair three nested about five feet from the edge of a sandy road frequently used on weekends by hikers and passing automobiles. During early incubation, a person or dog walking by the tree caused the female to immediately leave the nest; however, she remained on the nest if a car passed. After heavy incubation began, passing individuals and dogs seldom disrupted her incubation activities.

Hatching—In one nest with three eggs, hatching extended for two days. The third egg did not hatch and remained in the nest with the two nestlings for at least five days.

The nestling flycatcher at hatching has tufts of creamy-colored feathers in various areas of the dorsal portion of the body. The nestlings characteristically contain a considerable amount of blackish pigment, especially on the dorsum. Dawson (1923) said "the chicks are black for a few days after hatching, with some outcropping of white down." We, however, cannot agree entirely with Wheelock's (1904) statement that the young flycatcher at hatching is salmon-pinkish in color. Two nestlings weighed 1.1 and 1.5 grams on the day of hatching.

Parental care of the nestlings—Both sexes fed the nestlings. The male and female fed the young 11 and 8 times, respectively, during 185 minutes at one nest with two nestlings, the oldest two days of age. The female continued to brood the young in the early stages of nest life. The male often fed the brooding female in the same manner as during incubation. She would eat or pass the food to the nestlings by raising up in the nest giving the feeding notes. The frequency of feedings of the female by the male diminished after the young were present. In one nest with three nestlings, the female and the male made 6 and 4 trips, respectively, during 64 minutes of observation in the late morning. In another nest, the female made only two feedings in 110 minutes to the one nestling that had hatched that morning. Both feedings occurred as the female began an attentive period. The male flycatcher did not feed the nestlings or the female during this period.

Both sexes removed fecal sacs. At a nest with two young (0 and 2 days old), the male and female each removed and ate three fecal sacs during 122 minutes of observations.

Observations of the later phases of the nesting activities were limited since two of the first nests were disrupted by unknown causes. One nest had its contents (two well-developed nestlings and one unhatched egg) completely removed, although the structure remained in perfect condition. The other

nest was abandoned for unknown cause the day two eggs hatched. The young lay dead in the nest along with an unhatched egg, but the adults were observed in the area. A second nest of the pair was under construction 6 May, four days after discovery of the dead young.

SUMMARY

A study was made of breeding activities of Vermilion Flycatchers in a mesquite woodland, near Mesa, Maricopa County, Arizona. Hostile behavior in territorial defense is described. Four distinct vocalizations were recognized; the song is a function of the male. Data on nest building, clutch size, egg-laying, incubation period and behavior, hatching, and parental care of the nestlings are given.

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PUBLICATION NOTES AND NOTICES

IDENTIFICATION GUIDE TO EUROPEAN PASSERINES. By Lars Svensson. Naturhistoriska Riksmuseet, Stockholm, Sweden. 1970: 4 × 7½ in. 152 pp. many text figs. 15 Swedish Kroner.

A pocket guide to identification, sexing, and aging of birds for banders, and those studying museum skins. Approximately 15 North American species are included.

BIRDS OF THE BOZEMAN LATILONG. By P. D. Skaar. Privately published, 1969: 8½ × 11. 132 pp., mimeo, no price given. (Obtainable from P. D. Skaar, 501 S. Third St., Bozeman, Montana.

An annotated list of 277 species listed between 45° and 46° N latitude and 111° and 112° W longitude (latilong).

CALIFORNIA BIRDS—(A new periodical). Published by the California Field Ornithologists, Clifford R. Lyons, Treasurer, 6424 Mt. Adelbert Drive, San Diego, California 92111. Annual dues \$5.

This is a most welcome addition to the list of state ornithological journals for a state with a large body of active bird students. Volume 1, No. 1, 1970 contains an updated checklist of the Birds of California.

GENERAL NOTES

Additional notes on the plumages of the Redhead (*Aythya americana*).¹—During my study of the plumages of Redheads (Weller, Wilson Bull, 69:5–38, 1957), several confusing observations were made on the plumages of young males in the fall. These probably were not properly interpreted, and this note is a re-evaluation of my earlier study in the light of observations by Humphrey and Parkes (Auk, 76:1–31, 1959), and a report of a brief experiment designed to better appraise the early plumages of male Redheads.

My earlier comments on the young male (1957:23) were: “Many males have brownish-red feathers in their lores and cheeks at eight weeks of age; these are present in all males at nine weeks”. . . . “At 14 weeks, the male’s head is more chestnut than buffy brown. . . .” The latter plumage is illustrated in the color plate facing page 5, which also shows the acquisition of post-juvinal male plumage in the chest, sides and scapulars. The color of the head in this plumage more nearly resembles that of adult males in “eclipse” plumage than of adult males in nuptial plumage.

At that time I assumed that the early feathers of the nuptial plumage merely were less definitive in color and size. Because I was unable to observe these changes throughout the winter, the transition was less noticeable. A comparison of skins from birds taken in fall and spring shows a rather marked difference in brilliance of the red color, purplish iridescence and length of the head feathers.

In an attempt to better analyze the transition from the tan-headed juvenile to the red-headed adult plumage and to determine the status of intermediate plumages in females, detailed observations were made on eight captives during the fall of 1966; five were males, three were females. These birds were obtained from the Northern Prairie Wildlife Center of the Bureau of Sport Fisheries and Wildlife for which I am indebted to Harvey Nelson, Director, and Charles Dane, Wildlife Biologist. Arnold O. Haugen transported the birds from Jamestown, North Dakota, to Ames, Iowa, where the birds were housed outdoors. Thanks are due Eldon Greij, Loren Bates, and Robert Bergman for assistance in care of birds and in recording data.

On receipt on 8 October, birds were about 13 weeks old. All were examined for plumage status and molt, and selected feathers or tracts were clipped for identification. Although clipping did not permit identification of all feathers of a particular tract, the presence or absence of these feathers aided in determining the number of plumages involved. To quantify the degree of molt, intensity was scored on a scale of: 0 (none), 1 (little) or 2 (much). Each feather tract was examined by lifting the feathers with a forceps. When less than one fourth of these probes showed new feathers, molt was recorded as little. When more than one fourth showed new feathers, it was termed much. Tracts were examined approximately monthly from 8 October 1966 to 27 May 1967. Data from one male are deleted because its chronology of molt was markedly delayed.

All birds received were in dominantly juvenal plumage but were involved in a post-juvinal molt of the entire head and much of the body. This molt continued through December, but there was little or no molt in most birds in January (Fig. 1). Another molt from late February through March involved both the head and body of females but mainly the body of males. Then the eclipse plumage started to develop in males in early

¹ Journal Paper No. J-6122 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 1504.



FIG. 1. Postjuvinal molt indices for four male and three female Redheads.

to mid-April, presumably because of the lack of conditions that would produce a normal breeding cycle. In addition, some infrared lights used in January may have induced early plumage development. This early molt in males made it difficult to interpret the third plumage acquired in early spring by females.

Clipping was done either when birds were received in October or during mid-January when their first molt ceased. The most significant results were from birds mass-clipped with a scissors in each feather tract. The following individual examples help to explain the curves that show an average of all molt of males and females (Fig. 1) and the curves for selected areas (Fig. 2).

Males.—It appears that males actually have two head molts following the juvenal plumage and that both are completed by early January concurrent with the body molt. The first head molt occurs in October and produces brownish-red head feathers longer than those of the juvenal plumage but which lack the length, color, and iridescence of those that develop in late November and early December. Male No. 86 was clipped on 8 October, and all clippings on the head were gone by 3 December. Head molt continued in January. These molts are so continuous that no stopping points are available to use as a base to appraise the extent of the molt or number of plumages. Males Nos. 78 and 92 both were mass-clipped on 29 January following completion of the extensive double head molt. Both still had evidence of clipping on the head in early April suggesting that few additional red feathers developed. Thereafter, brown feathers of the eclipse plumage developed on the head and body and molt continued through May.

The juvenal body plumage and tail were replaced with a somewhat dull but adult-like plumage by late December during the period when two head molts occurred. Some clipped body feathers of male No. 86 were retained from 8 October until 18 February and clipped mantle feathers existed until late May, but these could have been feathers of the first non-nuptial plumage.

The second period of body molt in late February and March was much less widespread than in females and involved mostly the scapulars and side (Fig. 2). Whether this was a complete renewal of the body plumage (into nuptial) or a partial body molt

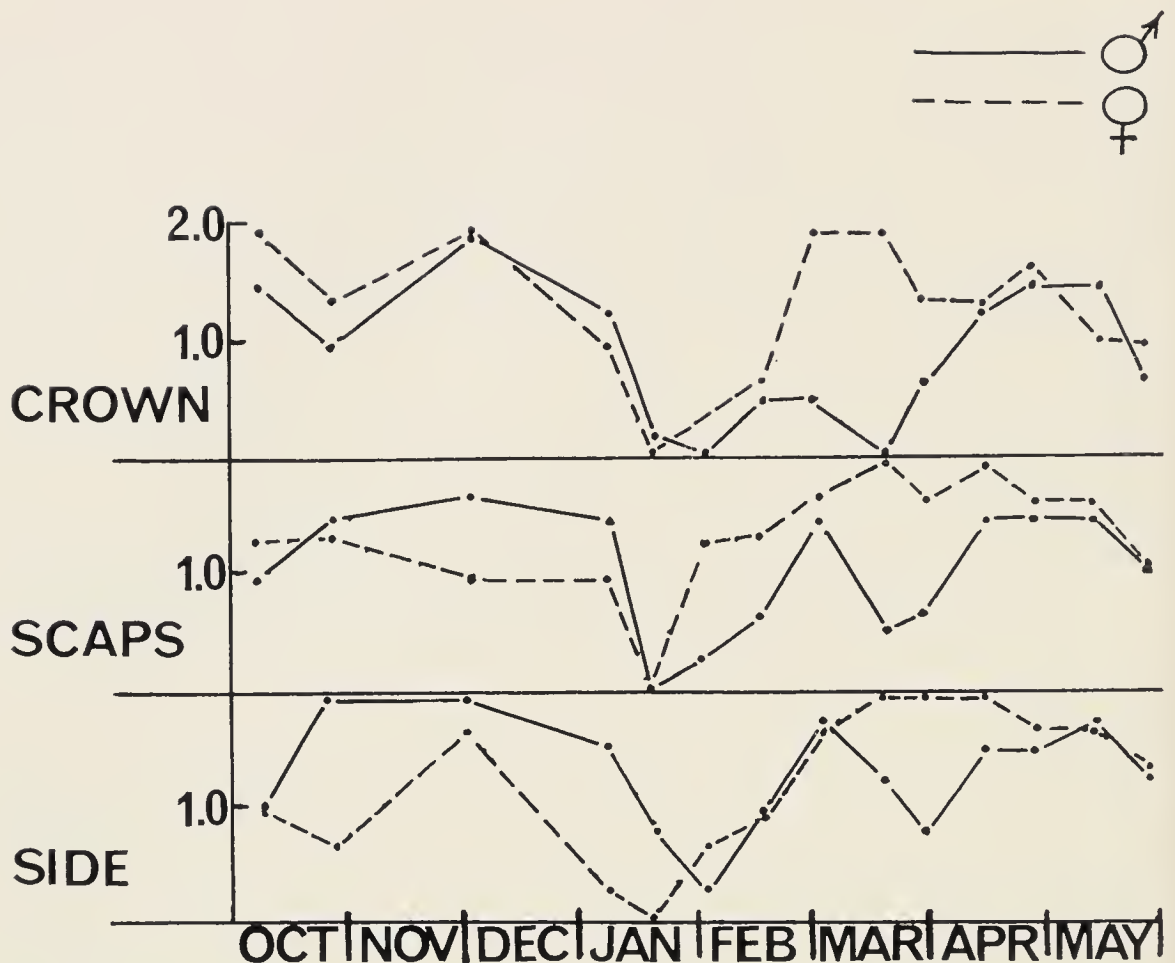


FIG. 2. Molt indices for selected feather tracts of four male and three female Redheads.

started in fall and finished in the spring is uncertain but there is no conspicuous change in body color during this period.

Females.—All feather tracts of female No. 77 were clipped on 8 October. By 3 December, all clipped feathers had been replaced on the head, chest and side but a few were present in the scapulars. All were gone by 21 January, but the posterior one-third of the belly still appeared to be dominantly juvenal.

A few feathers on all tracts of female No. 93 were marked and clipped on 8 October. These were gone by 3 December, and she completed a major molt on the head, neck and entire body by 7 January; at that time she was clipped again. Another molt started subsequently and the clipped head feathers were gone by 17 March; most clipped body feathers were replaced by 1 April except those of the mantle.

These two observations and Figures 1 and 2 suggest the following pattern in females: The juvenal head and body plumage is replaced by the first non-nuptial plumage by early January but some juvenal feathers may persist on the lower belly and venter. Possibly the timing of these plumages was influenced by captivity. A second molt occurred in late February and early March and presumably represents the pre-nuptial molt of the head, side and scapulars. The female became more rufous brown at this time as noted in wild birds (Weller, 1957:26). Subsequent molt in April and May was assumed to be the non-nuptial plumage but modifications of timing make the normality of this uncertain.

This sequence needs further study in both young and adult females. It is possible that a transient plumage occurs in females as it does in males but it could not be discerned from feather colors. Oring (Auk, 85:355-380, 1968) found a brief first non-nuptial (basic) plumage in autumn, nuptial (alternate) in winter and early spring, and a second non-nuptial in the early summer pre-nesting period of hen Gadwalls (*Anas strepera*). This would subsequently result in a pattern in adult females which is comparable to males except that females acquire the non-nuptial prior to nesting whereas males acquire it after breeding (R. Palmer, pers. comm.).

Too little data are available in this study to draw conclusions on complete sequences of plumages, but there is little question that the first non-nuptial plumage is present in both sexes. New techniques are needed to study the extent of these plumages in different tracts (and perhaps within tracts), the apparent inconsistency in number of feather generations per follicle, and the overlap of these plumages.—MILTON W. WELLER, Department of Zoology and Entomology, Iowa State University, Ames, Iowa 50010, 20 January 1969.

Observations on premigratory movements of hand-reared Mallards.—In July and August of 1968 a total of 301 four to five-week old Mallard (*Anas platyrhynchos*) ducklings were released in southern Wisconsin. These birds were hatched at the Delta Waterfowl Research Station in Manitoba, Canada from eggs collected from a captive wild flock of Mallards.

An analysis of the first fall band returns of these released juveniles shows that 18 were shot between 5 October and 26 October. During this premigratory period 15 of the recoveries were north of the release site and only three south of it (Fig. 1). This northward movement must have taken place sometime between the onset of flying in these young birds (about the second or third week in August) and the time when they

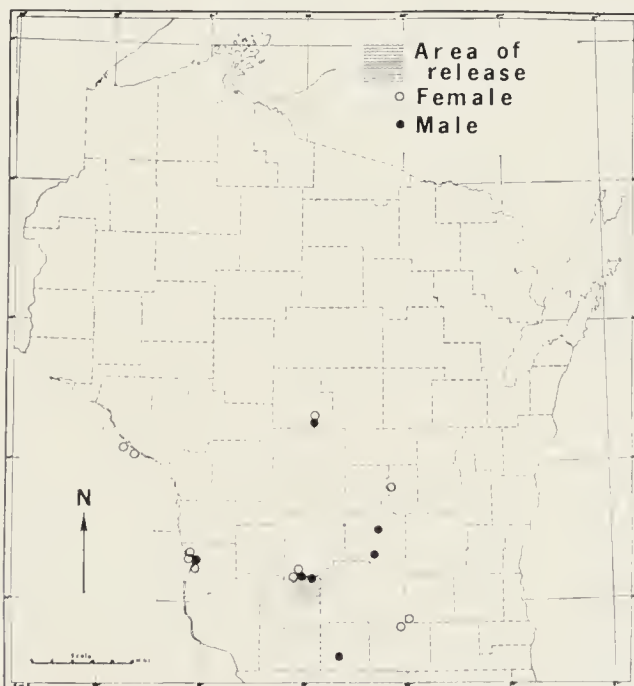


FIG. 1.

were shot. The average distance travelled by these birds during this time interval was 51.3 miles.

Bellrose (Bird-Banding, 29:75-90, 1958) found that wild Mallards released on clear days in unfamiliar terrain headed north no matter what time of the year they were released. The data reported here support these findings. They also indicate that this phenomenon may be shown by hand-reared birds as well as pure wild Mallards, and that this may be a long distance as well as an immediate orientation.—JAMES J. ZOHREK, *Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin. 2 August 1969.*

Trumpeter Swan carrying young.—This observation describes a Trumpeter Swan (*Olor buccinator*) cygnet riding on the back of an adult. Although Delacour and Mayr (1945) as quoted in Banko (The Trumpeter Swan, its history, habits and population in the United States. N. Amer. Fauna, No. 63, 1960) state that Mute (*Cygnus olor*) and Black-necked Swans (*Cygnus melancoriphus*) generally carry young on the back and other swans have this habit, Banko added that this behavior has not been reported in Trumpeter Swans.

Trumpeter Swans were transplanted from Red Rock Lakes National Wildlife Refuge, Montana to Lacreek National Wildlife Refuge, South Dakota in 1960 (Monnie, J. Wildl. Mgmt. 30:691-696, 1966). Two cygnets were produced in 1963 and reproduction increased to 15 cygnets reaching flight age in 1968.



FIG. 1. Trumpeter Swan carrying cygnet.

On 8 June 1969 at 18:30 a pair of Trumpeter Swans with five cygnets was surprised in a narrow borrow ditch adjoining a 531-acre marsh in which the pair had nested. Cygnets swam between the adults as the brood progressed down the ditch. Soon after, one cygnet swam around to the anterior end of an adult and climbed onto its back. The cygnet quickly turned around, sat down and began preening. Both adults were alerted to my presence and disregarded the preening cygnet (Fig. 1). Four other cygnets remained in the original swimming position. The swans were motionless in the water watching me or were swimming down the ditch during the next 15 minutes. The riding cygnet continued preening for five minutes and then returned to the other cygnets swimming between the adults. An opening in dense cattail provided an escape route allowing the brood to swim out of view a few minutes later.—DONALD A. HAMMER, *Lacreek National Wildlife Refuge, Martin, South Dakota, 2 September 1969.*

Notes on the foods of juvenile Black-bellied Tree Ducks.—Studies of waterfowl food habits traditionally emphasize the diet of adult game ducks (cf. Cottam, Tech. Bull. 643, U.S. Dept. Agr., 1939; Martin and Uhler, Res. Rept. 30 (reprinted), U.S. Fish and Wildl. Serv., 1951). Only more recently, however, have the diets of juvenile waterfowl been emphasized in the literature. Chura (Trans. N. Amer. Wildl. Conf. 26:121–134, 1961), for example, described the diet of maturing juvenile mallards (*Anas platyrhynchos*). Similarly, Bolen and Forsyth (Wilson Bull. 79:43–49, 1967) reported only the foods of adult Black-Bellied Tree Ducks (*Dendrocygna autumnalis*), and until now, even scant records were unavailable for young birds of this species.

Individual foods from both the crops and gizzards of two Black-bellied Tree Duck broods were examined volumetrically to determine basic trends in the diets of the young birds. The birds' ages were estimated from linear measurements of the middle toe, exposed culmen, and tarsus length following criteria developed by Cain (in press). These broods and other tree ducks were collected in 1966 and 1967 at Lake Mathis (= Lake Corpus Christi) in Live Oak and San Patricio Counties, Texas.

The foods of five 21-day old ducklings primarily consisted of *Echinochloa colonum* seeds; this food occurred in all of the gizzards and crops (100 per cent frequency within the brood) and with an average volume of 5.4 cc (crops) and 2.5 cc (gizzards). *Eclipta alba* (= *Verbesina alba*) seeds occurred in all of the crops and in 40 per cent of the gizzards; its volume was 0.1 cc or less in each case. Animal matter was found only in the crops (100 per cent frequency) and averaged 0.5 cc per bird.

The crops and gizzards of six 35-day old ducklings each contained *Sagittaria* tubers; the average volume for this food was 0.8 cc (gizzards) and 7.0 cc (crops). Trace amounts of *Heteranthera dubia* seeds occurred in some of these samples. Measureable amounts of animal matter were again largely limited to the crop samples; the average amount per crop was 0.6 cc.

The overall percentages of plant and animal materials in the diets of these broods are compared with similar data for a larger sample of adults in Table 1. The two adults tending the 21-day old brood contained only trace amounts of animal matter whereas the adult collected with the 35-day old brood lacked any evidence of animal food in its digestive tract.

The nature of the animal matter seems significant. Specifically, the animal foods taken by the younger brood included insects, spiders, snails (*Physa anatina*), and in one instance, a bivalve (*Sphaerium securis*). Of these, only the insects and spiders were

TABLE 1
COMPARISON OF OVERALL PLANT AND ANIMAL DIETS FROM THE CROPS OF JUVENILE
AND ADULT BLACK-BELLIED TREE DUCKS.

Age Group	Type of Food-Per cent	
	Plant	Animal
21-day brood	91.6	8.4
35-day brood	91.3	8.7
Adults ¹	94.4	5.6

¹ Data from Bolen and Forsyth (1967).

important foods, each occurring with 100 per cent frequency of occurrence. The insects included 14 families of which most (86 per cent) were primarily terrestrial.

Animal matter in the 35-day old brood included insects, snails, oligochaets, and single occurrences of an unidentified tick and freshwater shrimp. Nine insect families were represented of which only two (22 per cent) were primarily terrestrial taxa.

The incidence of terrestrial insects in the younger brood and the corresponding change to aquatic forms in the older broods suggests that young tree ducks are reluctant to submerge their heads while feeding. Additionally, the older tree duck brood fed heavily on submersed *Sagittaria* tubers whereas the young birds took plant foods either aerially or floating at the surface. Chura (op. cit.) found that young Mallards are at first hesitant to submerge while feeding and that they accordingly tend to avoid many aquatic invertebrates until their feeding behavior matures further. The few data now available indicate, however, that young Black-bellied Tree Ducks still in downy plumage apparently rely less heavily on animal foods than many other waterfowl species.

Several food items were identified with the gracious assistance of Francis M. Uhler and Harold D. Murray. The field work was supported by the Rob and Bessie Welder Wildlife Foundation and the School of Agricultural Sciences, Texas Tech University.—ERIC G. BOLEN AND JOHN J. BEECHAM, *Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409, 24 June 1969.*

Successful reconstruction of active Bald Eagle nest.—On 25 June 1969 an active Bald Eagle (*Haliaeetus leucocephalus*) nest in Itasca County, Minnesota, blew down during a violent rain storm (wind 65 mph). The nest, two 8-week-old eaglets, and the top two meters of the tree fell 18 m to the ground. The tree supporting the nest was a partially dead northern red oak (*Quercus rubra*) and had served as the nest supporting structure for 16 years. The nest was located 2½ m above the forest canopy on the dead portion of the tree and the parent birds had easy access from all directions.

The nestlings showed no apparent injuries and were kept for three nights in a makeshift nest box three m above the ground. This nest could not be seen from above the forest canopy. On 27 June an artificial nest was constructed adjacent to the trunk of the original nest tree on a large branch one-third m from the top of the tree. The base of the nest was constructed of six freshly cut poplar poles 1½ meters long which were nailed and criss-crossed on top of the branch. A two-meter square piece of 2½ cm chicken wire was then placed on top of this framework. A 1½ meter square piece of burlap was then placed over the larger sticks and on top of this were placed smaller

sticks and decayed woody material from the old nest. Fresh sphagnum moss (*Sphagnum* spp.) was then placed on top of the entire structure to prevent rain from washing away the woody material. This moss is commonly found in Bald Eagle nests in Minnesota.

The eaglets were fed small minnows (*Chrosomus* spp.) and pieces of yellow perch (*Perca flavescens*) periodically until they were placed in the artificial nest at 08:15 on 28 June.

The female parent had flown over the nesting area on 25 and 26 June, but neither the female nor the male roosted in the area of the fallen nest at night. At 10:38 on 28 June the female flew by the nesting area out of sight of the nest and gave a series of calls. At 12:15 the male parent flew directly over the nest and showed no change in attitude or in normal flight. At 15:30 the female parent flew over the nest and gave a long series of calls while circling the area nine times then left. The male was observed stretching his wings and preening while on an alternate nest 350 m north of the artificial nest. He showed no interest in breeding activities. At 21:00 (20 minutes before sunset) the female returned to a favored perch near the artificial nest and was harassed by a Broad-winged Hawk (*Buteo platypterus*). She issued a continuous series of calls for 20 minutes and flew seven circle flights. At 21:25 she flew to the nest tree, perched on top of it, and peered down at the nestlings. She then dropped gently to the artificial nest and exchanged a series of soft calls with the young.

A thunder storm occurred the night of 28 June. On 29 June both young were present with bulging crops, fresh bullheads (*Ictalurus* spp.) and ciscos (*Coregonus* sp.) were in the nest, and both parents flew circle flights around the nest for the entire period that the senior author was present at the nest. Activity at the nest was observed on 29 and 30 June and parents brought food regularly. To our knowledge this is the first time that an experiment such as this has been recorded in the literature for this species.

Both birds successfully fledged from the nest and were seen flying in the vicinity of the nest during the month of October.

This work was funded by grants to the senior author for Bald Eagle research from the Society of the Sigma Xi Grants-in-Aid of Research, and from the National Audubon Society.—THOMAS C. DUNSTAN, *Department of Biology, University of South Dakota, Vermillion, South Dakota (Present address: Department of Biological Sciences, Western Illinois University, Macomb, Illinois 61455)* and MELVIN BORTH, *RR 1, Coleraine, Minnesota 55722, 8 July 1969.*

Territorial conflict in the American Woodcock.—I reported in-flight, physical contact between two male American Woodcocks (*Philohela minor*) (*in* Sheldon, *The book of the American Woodcock*: 52, 1967). I believe that this was the first report of in-flight contact in this species although "tilting" has been reported in the European Woodcock (*Scolopax rusticola*) (Slater, *British birds with their nests and eggs*, V:106, 1898). This note presents additional details of the observation.

On 30 April 1961 I observed the courtship activities of two woodcock which had established singing grounds within 300 feet of each other in abandoned fields in Leverett, Franklin County, Massachusetts. The two males were displaying in an irregular sequence and the flights frequently overlapped in time. At 19:30 bird "B", whose ascending flight spirals had been gradually shifting on successive flights, flew directly over the spot where bird "A" had just plummeted to the ground. "A" flew without a pause after landing and ascended silently and nearly vertically (instead of in its normal gradual southerly flight route) to intercept the "B" bird. Physical

contact took place at an estimated height of 75 feet. The birds ascended perhaps another 25 to 50 feet while fluttering breast to breast. They then locked together and fell 50 to 75 feet before breaking apart. One bird flew off in straight level flight in a north-northwesterly direction, closely pursued by the other bird until they were lost in the deepening dusk. The entire encounter lasted only thirty seconds. Civil twilight ended at about 19:33; this coupled with a clear sky and rise of a full moon at 18:46 provided a good background against which the performing birds were clearly silhouetted.

After about five minutes a bird, that I believe to have been one of the original two birds, returned from the exact direction of departure and "peented" from the singing ground of bird "A." After its next flight it "peented" from the singing ground of the "B" bird. It continued to use these two grounds alternately. This alternate use, by a single bird, of both singing grounds continued for the next two evenings. For the remainder of the season only the singing ground of the "A" bird was utilized while that of the "B" bird remained untenanted. All elements of the performance except the in-flight contact have been described by others, although not in the complete sequence that I observed (Pettingill, *The American Woodcock*, *Philohela minor* (Gmelin): 287-291, 304, 1936; Pitelka, *Wilson Bull.*, 55:100, 105, 107-109, 113, 1943; Sheldon, *op. cit.*: 44, 62).

I use the term dual flight to describe the synchronized or responsive flight of two woodcock in close proximity in contrast to the normal courtship flight of the male when performed by two birds simultaneously (Bent, *U. S. Natl. Mus. Bull.*, 142:64, 1927) and the flight described by Forbush (*Birds of Massachusetts and other New England States*, I:388, 1925) which probably involved a female. Dual flight has been reported in the American Woodcock by Brooks (*Auk*, 52:307, 1935) the Speirs (Pitelka, *op. cit.*: 105) and perhaps best described by Bagg and Eliot (*Birds of the Connecticut Valley in Massachusetts*, 208, 1937). Pitelka (*loc. cit.*) has suggested that "double" flight is due to the accidental simultaneous initiation of song flight by two males. Dual flight in the European Woodcock has been reported by Bannerman (*The birds of the British Isles*, 9:110, 1961); Warwick and van Someren (*Scottish Naturalist*, 222:170, 1936) who believe dual flights to be those of male and female although as Pitelka (*loc. cit.*) notes there seems to be no clear evidence on the sex of participating birds and Slater (*loc. cit.*) who reports that "tilting" of two, or even three, birds together has been ascribed to pairing activities but Slater considers it playfulness since he observed "tilting" up to the end of May. However, Sheldon (*op. cit.*, 164) says the European Woodcock has two peaks of singing activity one in April and early May and one in July.

More work needs to be done on the problem of territoriality in the woodcock, but I believe that dual flight, at least in the American Woodcock, occurs too infrequently to consider it a normal part of pairing activity and too frequently to consider it as the coincidental initiation of song-flight by two males. Furthermore, dual flight differs from normal song-flight and in my observation coincidental flight is ruled out. I suggest that in the American Woodcock dual flight represents a high intensity aggressive confrontation between two territorial male woodcock that may be followed on rare occasions by actual in-flight combat.

I thank Dr. Stephen M. Adler of Mount Holyoke College for calculation of the time of sunset and moonrise at Leverett, Massachusetts.—FREDERIC W. DAVIS, *Fitchburg State College, Fitchburg, Massachusetts, 20 June 1969.*

Chuck-Will's-Widow in Connecticut.—On 26 June 1969 I found a Chuck-Will's-Widow (*Caprimulgus carolinensis*) dead on a road near Stoney Creek, New Haven County, Connecticut. This is the second specimen record of this species for Connecticut. The first specimen was found in New Haven, 10 miles west of Stoney Creek, on 17 May 1889 (Sage and Bishop, *The birds of Connecticut*, Connecticut Geol. and Nat. Hist. Survey, Hartford 1913). The bird is now in the Peabody Museum of Natural History, Yale University (No. 85435).

The bird was an adult female with the ovary slightly enlarged (five ova measured 2 mm in diameter) and it had little fat. It showed no body or tail molt but the first three primary flight feathers on each wing were new. The stomach was filled with 68 small white geometrid moths (*Ennomos subsignarius*) and six June beetles (*Phyllophaga* sp.). The stomach contents reflect the unusually high population peak of this geometrid moth that occurred in Connecticut during late June.—EUGENE S. MORTON, *Department of Biology, Yale University, New Haven, Connecticut, (Present address: Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone), 12 August 1969.*

Predation of a Black Rat Snake on Yellow-shafted Flicker Nestlings.—At 18:45 on 10 June 1968, five miles north of Burlington, Des Moines County, Iowa, I observed the predation of a black rat snake (*Elaphe obsoleta*) on a nest of half-grown Yellow-shafted Flickers (*Colaptes auratus*). Predation of rat snakes on birds is not unusual and predation on nestling woodpeckers has been previously mentioned (Nolan, *Wilson Bull.*, 71:381–382, 1959; Noland, *The Kentucky Warbler*, 36:29–30, 1960; Stickel, *Auk*, 79:118–119, 1962). Of particular interest in this case is the extraordinary climbing ability exhibited by this snake and the apparent passivity with which the adult bird let its nest be robbed.

The nest tree, a dead American elm (*Ulmus americana*) approximately four feet in diameter at breast height, had no bark and was worn quite smooth by weather. There were no branches on the tree between the ground and the nest branch, though the trunk was much convoluted near the base. There were no evident holes other than the nest hole and the tree did not appear to be hollow. The nest was about 20 feet above the ground in a branch extending southeast from the trunk at a 45 degree angle. At the nest entrance the diameter of the limb was approximately 15 inches. The only apparent way for the snake to have reached the nest was by climbing the smooth, featureless surface of the tree.

When first observed, the snake was in the nest with only the last eight inches of tail extending from the hole. A female flicker, presumably one of the parent birds, was perched quietly in a second dead elm 30 yards away in line of sight with the nest hole. This bird remained in its position for 45 minutes before it quietly left, never approaching the nest tree.

About five minutes after I discovered the nest the snake's head appeared in the hole with a young flicker in its mouth. The bird, being swallowed tail first, was about half the size of an adult, had contour feathers just emerging from their sheaths, and appeared to have just opened its eyes. The nestling was lifeless. At first staying tight against the surface of the limb, the snake slowly began weaving back and forth and slightly up and down from one side of the limb to the other. Two large swollen areas evidenced previous victims, presumably other flicker nestlings. The weaving and contortions about the nest hole appeared to be aiding in the swallowing of the third victim, though 20 minutes later the head and one wing still protruded from the snake's mouth. At this

point the snake withdrew into the hole (19:15) and did not emerge while it was still light enough to observe.

Black rat snakes are noted for their climbing ability (Johnston and Gaunt, *Kansas Ornithol. Soc. Bull.*, 12:22-23, 1961; Fitch, *Copeia*, 1963:649-658, 1963) and Surface (*Bull. Div. Zool., Pennsylvania State Dept. Agr.*, 4:113-208, 1906) found 30 per cent and Fitch (*op. cit.*) found 23 per cent of black rat snake food consists of birds or their eggs. Though normally adult birds would be difficult prey for a snake, an incubating or brooding adult, as well as nestlings and eggs, would be easier prey. A hole-nesting bird such as a woodpecker, while having a safer nest in many respects and an easier nest to defend, has no avenue for escape if surprised by an arboreal snake. Birds are not totally helpless in the face of such an adversary, and, may at times be successful in repelling the predator. Boone (1960. Masters Thesis, University of Kansas, Lawrence, Kansas) observed a male Red-bellied Woodpecker (*Centurus carolinus*) defending its nest against a black rat snake. Nolan (*op. cit.*) and Noland (*op. cit.*) describe possibly fatal attacks on arboreal snakes by nesting Pileated Woodpeckers (*Dryocopus pileatus*). Fitch (*op. cit.*) mentions that Blue Jays (*Cyanocitta cristata*) have also been seen attacking black rat snakes.

A second defense against arboreal snakes, or at least a distraction for the snake is a mobbing reaction by birds. Once a snake has been observed by a bird, cries of alarm generally attract other birds. Fitch (*op. cit.*) reported such aggregations involving several species.

In the case of the Yellow-shafted Flicker, there was no evidence of nest defense or mobbing, but either or both may have occurred before the snake reached the hole. Though the snake was completely hidden within the nest hole from 19:15 to dusk, knowledge of the snake's presence or fright from an earlier encounter with the snake apparently kept the flicker from returning to the nest to feed or brood its young.—JEROME A. JACKSON, *Museum of Natural History, University of Kansas, Lawrence, Kansas* 5 May 1969. (Present address: Dept. of Zoology, Mississippi State University, State College, Mississippi 39762.)

Wing flashing in a Brown Thrasher and Catbird.—Wing flashing has been frequently reported for Mockingbirds (*Mimus polyglottos*) and occasionally for other Mimidae (Whitaker, *Wilson Bull.*, 69:361, 1957; Batts, *Auk*, 79:112, 1962; Horwich, *Wilson Bull.*, 77:264, 1965; Ricklefs, *Wilson Bull.*, 78:47, 1966). Horwich stated that this behavior is a response to a strange situation or potential predator. This has been supported by Hicks (*Auk*, 72:296, 1955) who observed wing-flashing by a Mockingbird in response to a blacksnake (*Coluber constrictor*) and by Selander and Hunter (*Wilson Bull.*, 72:341, 1960) in response to a Screech Owl (*Otus asio*).

On 29 June 1969 a Brown Thrasher (*Toxostoma rufum*) was first seen as it scolded a 32-inch long buttermilk snake (*Coluber constrictor anthicus*) in Nacogdoches County, Texas. Within 3 minutes six Blue Jays (*Cyanocitta cristata*), three Cardinals (*Richmondia cardinalis*), two Catbirds (*Dumetella carolinensis*), and two Carolina Wrens (*Thryothorus ludovicianus*) joined the Brown Thrasher. The Brown Thrasher extended its wings outward and slightly upward at the rate of once every 14 seconds. The extension was accomplished with a slight hitch when the wings were two-thirds extended. The tail was spread and held straight out behind.

The two Catbirds both spread their tail and extended their wings while hopping around excitedly near the Brown Thrasher. Both Catbirds extended their wings in a

single motion but held them out 4-5 seconds as compared to the Brown Thrasher which kept its extended only 1-2 seconds. None of the other birds present extended their wings. After 20 minutes the snake crawled out of sight in some dense bushes and all the birds left the immediate area.—EDWIN D. MICHAEL, *Biology Department, Stephen F. Austin State University, Nacogdoches, Texas 75961 (Present address: Division of Forestry, West Virginia University, Morgantown, West Virginia 26506). 28 July 1969.*

Re-evaluation of two supposed hybrid birds.—In 1967 Keith L. Dixon requested information on a reported hybrid chickadee supposed to be in the U. S. National Museum. The specimen could not be found at that time but it was recently discovered in the course of routine expansion and rearrangement of the Paridae in the USNM collection. When I informed Dr. Dixon that in my opinion the bird was not a hybrid he urged preparation of a note indicating the apparent basis of the record. It seems appropriate to include comments on a White-crowned Sparrow specimen also misidentified as a hybrid, a situation of which I have been aware for some years.

Parus atricapillus × *P. gambeli*.—This hybrid combination was reported by Suchetet (1897) on the basis of a specimen in the U. S. National Museum about which Robert Ridgway had written him. Ridgway is quoted as saying that the bird was in every respect exactly intermediate between the two forms. No other information about the specimen is given. The record is repeated by Cockrum (1952) and Gray (1958) without comment.

Specimen No. 60433 in the U. S. National Museum almost certainly is the bird about which Ridgway wrote. The locality on the label is "Bitter Cottonwood;" the museum catalog expands this to Bitter Cottonwood Creek, Wyoming Territory. The bird, which is not sexed, was collected by H. D. Schmidt on 14 August 1870 and was originally identified as *Parus atricapillus*. The notation "& *P. montanus (Hybrid!)*" was later added to the label by Ridgway; the name *montanus* as used in that instance refers to the present *Parus gambeli*. The specimen is in fairly good condition, but the head is somewhat flattened.

Contrary to the remark attributed to Ridgway, this specimen appears to be typical of *P. atricapillus* in every respect of size, proportion, bill shape, and color, except that it possesses traces of white superciliary stripes. The feathers that make up these stripes are merely edged with white rather than fully white tipped as in *P. gambeli*, and the stripes do not join across the forehead as they do in that species. A relatively small number of feathers is involved in the stripes, which do not extend as far posteriorly as in typical *gambeli*. I believe that this bird is best considered an aberrant example of *Parus atricapillus* rather than a hybrid between that species and *P. gambeli*. Wetmore (1931) mentions examining "a number" of Black-capped and Carolina Chickadees (*P. carolinensis*) with one or more white feathers at the junction of the auricular and crown patches, where the stripe on *P. gambeli* occurs.

Zonotrichia leucophrys × *Z. albicollis*.—This hybrid combination was twice reported by Abbott (1958, 1959) on the basis of a single male bird taken at Fort Belvoir, Virginia, on 5 January 1958. The specimen is No. 468554 in the USNM.

James K. Lowther and I examined this specimen on separate occasions in 1962 and we independently concluded that it is an example of *Z. l. gambelii* and not a hybrid. The "very large and broad loreal area" cited by Abbott (1959) as a criterion for the hybrid determination results in large part from the make of the skin.

The bend of the wing is not "lemon yellow" as stated by Abbott (op. cit.) nor is it the same as the color of the bend of the wing in *albicollis*. The bend of the wing on the bird in question is faintly tinged with yellow and but slightly more yellowish than normal for *Z. l. gambelii*, well within the range of color shown in the species. The other features of the bird cited by Abbott are within the range of variation of the white-crown. A whitish throat patch, present in the bird under consideration and the feature at first most suggestive of hybridization although not specifically mentioned by Abbott, is a not uncommon attribute of the White-crowned Sparrow; in the bird under consideration, it is merely more extensive than usual. There is no evidence of the black malar stripes which often serve to set off the throat patch in the White-throated Sparrow.

Sibley (1956) reported a Golden-crowned Sparrow (*Z. atricapilla*) with a white throat, an occurrence strikingly similar to the one under discussion. He also mentioned two others of that species with some white in the throat and a *Z. l. gambelii* with a very pale throat. Sibley wrote: "These facts suggest that there is a normal genetic basis for white in the throat plumage of *atricapilla*. It seems probable that the white throat in this otherwise normal specimen of *atricapilla* is due, not to hybridization, but either to the chance coalition of a larger than usual number of multiple factors affecting white throat plumage or to a mutation which affected the deposition of pigment in the feathers of this area." With the substitution of the name *leucophrys* for *atricapilla*, that statement aptly fits the present situation.

I am grateful to Keith L. Dixon, Roxie C. Laybourne, and Susan Covington for comments and assistance in the preparation of this manuscript.

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The avifauna of the Sand Draw local fauna (Aftonian) of Brown County, Nebraska.—The first birds known from the Sand Draw local fauna were reported by Jehl (*Auk*, 83:669-670, 1966). The fauna is considered to be Aftonian (first interglacial) in age (see McGrew, *Field Mus. Nat. Hist., Geol. Ser.*, 9:34-35, 1944, and Hibbard, *Michigan Acad. Sci., Arts, and Letters*, 62nd Ann. Rept., p. 19, 1960), and as Jehl (op. cit.) pointed out, "None of the avian fossils contradict this interpretation, and the presence of a large stork seems to support the view that this fauna lived in a warm, interglacial period." The fossils reported herein were collected by C. W. Hibbard of The University of

Michigan Museum of Paleontology and his field party during the summer of 1968. The birds are as follows:

Anas discors Blue-winged Teal.—Three bones, a complete but damaged left humerus (UMMP No. V57157 from SW $\frac{1}{4}$, NW $\frac{1}{4}$ Sec. 25, T31N, R22W, Brown County, Nebr.), the distal end of a right humerus (UMMP No. V57020, from SE $\frac{1}{4}$, SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 1, T31N, R23W, Brown County, Nebr.), and a complete right coracoid (UMMP No. V57158, from the same locality as V57157) represent this species. In total length the humerus measures 62.3 mm, the coracoid, 33.7 mm.

Laterallus sp. Small rail.—The distal end of a right coracoid (UMMP No. V57019, from W $\frac{1}{2}$, NW $\frac{1}{4}$, Sec. 25, T31N, R22W, Brown County, Nebr.) represents a small rail similar to the living *Laterallus* rails but is too fragmentary to permit positive identification to species.

Speotyto cunicularia intermedia, new subspecies. Sand Draw Burrowing Owl.

Type.—Fig. 1. Proximal 33 mm of left tarsometatarsus (UMMP No. V57018, from NW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 26, T31N, R22W, Brown County, Nebr.). Collected by C. W. Hibbard and field party, summer, 1967.



FIG. 1. The distal ends of the tarsometatarsi of, from left to right, the type of *Speotyto cunicularia megalopeza*, *S. c. intermedia*, and Recent *Speotyto cunicularia hypugaea* (UMMZ No. 99406).

Diagnosis and Comparisons.—This tarsometatarsus represents an owl belonging to the genus *Speotyto*, similar to the Recent *S. cunicularia* in all characters except size of trochleae and shaft which are more robust in the fossil. Ford (Condor, 68:472-475, 1966) described *S. megalopeza* from the Rexroad formation of the Upper Pliocene of Kansas as, "Morphologically similar to *S. cunicularia* but distinct in having slightly more robust trochleae and a much wider and thicker shaft." The Sand Draw fossil is a perfect intermediate

between the Recent *S. cunicularia* and the Pliocene *S. megalopeza* in robustness, and in my opinion *S. megalopeza* and the Sand Draw Burrowing Owl represent a temporal cline leading to the Recent *S. cunicularia*. I therefore recommend making *S. megalopeza* a temporal subspecies of the Recent *S. cunicularia* to best reflect its relationships.

Measurements.—The Sand Draw fossil measures in width across trochleae, 7.6 mm; width of shaft, 3.3 mm, measured 9 mm from distal surface of groove of middle trochlea; and depth of shaft at same level, 2.2 mm. Corresponding measurements for the type of *S. megalopeza* are, respectively: 7.6 mm, 4.0 mm, and 2.3 mm. The measurements that Ford (op. cit.) gives, “. . . for the largest (UMMZ No. 99406) of 13 individuals of *cunicularia* examined are, respectively, 7.6 mm, 3.2 mm, and 1.9 mm.”

Speotyto cunicularia megalopeza also is known from the Fox Canyon local fauna of the Rexroad formation, Upper Pliocene of Kansas (Ford, op. cit.), and from the Hagerman local fauna of the Glens Ferry formation, Upper Pliocene of Idaho (Ford and Murray, Auk, 84:115–117, 1967). The modern form, *S. cunicularia*, has been reported from the McKittrick and Rancho La Brea deposits of the late Pleistocene of California (Wetmore, Smith. Misc. Coll., 131(5):87, 1956).

Passerines.—Several fragmentary bones represent small passerines but are unidentifiable to family.

Egg shells are commonly recovered from the matrix.

The presently known avifauna of the Sand Draw local fauna is as follows:

Horned Grebe	<i>Podiceps auritus</i>
Stork	cf. <i>Ciconia maltha</i>
Canada Goose	<i>Branta canadensis</i>
Trumpeter Swan	<i>Cygnus buccinator</i> ¹
Blue-winged Teal	<i>Anas discors</i>
Bufflehead	<i>Bucephala albeola</i>
Small Rail	<i>Laterallus</i> sp.
Burrowing Owl	<i>Speotyto cunicularia intermedia</i>
Small Passerines	

I wish to thank Drs. C. W. Hibbard, R. W. Storer, and H. B. Tordoff for their criticism of the manuscript, and Karoly Kutasi for taking the photograph for Figure 1. Financial support for Dr. Hibbard's field work in Nebraska was provided by a grant from the National Science Foundation (GB-5450). My research was supported by a grant from the National Science Foundation, GB-6230, to N. G. Hairston, The University of Michigan, for research in Systematic and Evolutionary Biology.—J. ALAN FEDUCCIA, *The University of Michigan Museum of Zoology, Ann Arbor, Michigan*. (Present address: *Department of Biology, Southern Methodist University, Dallas, Texas*), 5 April 1969.

¹ A fragment of a tarsometatarsus (Frick prospecting loc. No. 263) from the Frick Collection of The American Museum of Natural History has been identified by Patricia V. Rich of the A.M.N.H. Dept. of Paleontology as close to the Recent *C. buccinator*.

ORNITHOLOGICAL NEWS

Inflation makes no exceptions for scientific societies, and at the recent meeting of the Council it was reluctantly voted to raise the dues. For 1971 membership dues in the Wilson Society will be \$8 for Regular Members, \$10 for non-member and institutional subscriptions, and \$15 for Sustaining Members. The contribution for Life Membership will go up to \$200, but anyone making the initial installment on a payment for Life Membership before 31 December 1970 can do so at the old rate. In return for this increase in dues it is our hope to make the *Bulletin* larger, and to reduce the long delay time in publication of papers.

The inside front cover of each issue of the *Bulletin* carries information about the Josselyn Van Tyne Library, one of the unique features of The Wilson Society. Each member should, then, be aware of the opportunity that he has to borrow books from the Library, but the Library Committee reports that in the 1969-70 year only 32 people availed themselves of this privilege. Perhaps cover material does not get read, and perhaps this notice will remind our members of the existence of the Library, which is a remarkably complete collection of the ornithological literature, journals and books, both technical and popular. With new book prices what they are today it would seem that many members would be willing to pay the return postage to Ann Arbor for even the most casual reading.

Some time ago an anonymous donor arranged for an award for non-professionals to be known as the Margaret Morse Nice Award. Regrettably, and surprisingly, there were no applications for this award in 1970. In the entire membership there must be at least one person who could use \$100 to help out his ornithological studies, and who meets the requirement of not being affiliated with a college or university.

We have received notice of the death of two longtime members: Life member Dr. Mary Juhn of Beltsville, Maryland on 3 May 1970 and James L. Baillie of Toronto, Ontario on 29 May 1970.

The Society has been the beneficiary of a gift for the purpose of awarding a monetary prize of \$150 for the best paper and \$50 for the second best paper appearing in *The Wilson Bulletin* during one calendar year. A committee of three, one of whom will be the Editor, will be appointed to judge the papers.

In June 1970, the Siam Society issued a memorial number of its *Natural History Bulletin* in honor of the late Herbert G. Deignan, an authority on the Birds of Southeast Asia, especially Thailand. He was Secretary of the American Ornithologist Union from 1959 to 1961.

The 200-page issue includes papers by friends and colleagues of Deignan's, covering subjects in which he was interested.

Copies may be obtained for \$2.50 plus 50¢ Seamail postage from the Siam Society, 131 Lane 21, (Asoke) Sukhumvit Road, P. O. Box 65, Central, Bangkok, Thailand.

ORNITHOLOGICAL LITERATURE

A COMPARATIVE STUDY OF THE BEHAVIOR OF RED-WINGED, TRICOLORED, AND YELLOW-HEADED BLACKBIRDS. By Gordon H. Orians and Gene M. Christman. University of California Publications in Zoology, Vol. 84, 1968: 81 pp., 2 pls., 30 figs., 10 tables. \$3.00.

The purpose of this study is to "analyze the influence of the striking differences in social organization upon the evolution of behavior" in three marsh-nesting icterids. Displays (other than vocalizations) of all three species are described in 19 pages, nine of which are comprised of excellent sketches by the junior author. Vocalizations are described in 25 pages in which appear 16 figures of sonographs. Comparison of all displays and vocalizations is achieved by a system of scoring "based upon the conspicuousness of the displaying bird." Points are added according to the degree of erection of plumage of different parts of the body, spreading of wings and tail, etc., and this information is presented in tabular form. This is an interesting way of giving emphasis to the importance of the display components and their possible combinations. Displays and vocalizations of all three species are related to specific stages of the breeding cycle in six figures.

Displays and vocalizations are considered to function primarily to communicate information. Based on a set of assumptions, namely, that information of environmental, social, identifying, and locating nature is being communicated, an analysis is made, but for the male Red-winged Blackbird only, of the amount of information transferred by each display and vocalization.

An "evolutionary analysis of blackbird behavior" is based on the "importance of five major factors on the evolution of similarities and differences both within species (especially sexual differences) and between species." These factors are: species recognition, social organization, habitat, plumage patterns, and motivational changes. This interesting discussion covers 13 pages.

In a concluding section the authors speculate briefly on the origins of blackbird displays. Landing movements, it is suggested, may have given rise to aspects of flight displays and displays accompanying basic song; vocalizations "probably all have been ultimately derived from breathing movements. . . ." Caution is advised (p. 75) in interpreting behavior in relation to causation: "Behaviorists attempting motivational interpretations are subject to errors comparable to those of a paleontologist uncritically assuming that a group of organisms necessarily evolved where most living members occur." A forewarning of this point of view is given in the introduction, the authors noting that they have largely omitted motivational analysis in the belief that descriptive field studies can yield only "crude speculation" in this respect. Evidently, something more than "single frame analysis of over 2,000 feet of motion pictures," a large series of recordings of vocalizations, and field observations during eight breeding seasons is necessary in order to obtain data that will yield information on motivation.

Perhaps the authors are simply more candid than most of us, their uncertainties in this behavioral study being freely admitted: "Some behaviors. . . are *exceedingly difficult* to understand" (p. 54); ". . . it is *exceedingly difficult* to measure information transfer between individuals. . ." (p. 57); ". . . the risks and the benefits of social behavior patterns are *exceedingly difficult* to measure. . ." (p. 62); ". . . since many of the displays are associated with a wide variety of vocalizations we have found it *exceedingly difficult* to

fit them into such a scheme. . ." (p. 74); ". . . song and other territorial vocalizations. . . and their associated displays should evolve primarily internal control and should be *exceedingly difficult* to analyze. . ." (p. 75). (Italics mine).

This work was evidently carefully proof-read for there are few typographical errors. Some of the graphs, e.g., Figs. 16, 19 and 24, are poorly set, and the illustrations of Wing Flipping (Fig. 4) have reversed captions. Figure 4d illustrates Wing Flipping in the female Redwing (as drawn from a photo in Nero, 1956:14).

The section on displays was of particular interest to me since, as the authors state, frequent references were made to reports by me on behavior of two of the species concerned, the Redwing and the Yellowhead (Wilson Bull., 68:5-37, 129-150, 1956; Wilson Bull., 75:376-413, 1963).

In view of the significance which the authors attach to the number of displays in each species and especially the number and kinds of components in what are called equivalent, comparable, or analogous displays, it is important to establish that such displays are comparable and disparate. Some questions may be raised in this respect. The male Yellowhead is said (p. 7) to have a flight display that is similar to the "Flight-song" of the male Redwing, though it differs in that it is always silent. It also differs from the Redwing in that it is given only over the territory though in the latter it is also given upon leaving and returning to the territory. Further, it is said to differ in that it often leads to an elevated wings display upon landing from which often a nest-site demonstration follows. This display, though differing from the "Flight-song" of the Redwing in three major respects, is treated as a corresponding display (Tables 2 and 3, pp. 50-53).

A second "territorial flight display" in the Redwing (p. 7) is called "Fluttering Flight. . . . After landing the male commonly continues the display while perched as the Defensive Flutter. . . ." The latter (p. 16), considered a "perched analog" of the former, "is most common during the early stages of territory establishment and when the females are arriving." This display appears identical to behavior that some observers have regarded as indicative of sexual excitement. And note that the "Si-si-si" call accompanying Defensive Flutter (p. 45-46) "may not be really distinct from the *Ti-ti-ti* [precopulatory] call" (p. 46). No reason is given for the reference to defensive behavior, a seemingly inappropriate term especially in a paper which attempts to avoid motivational aspects. In any case, the appearance of a display ("Flutter") both when perched and when in flight would not seem to warrant description and use as two separate displays.

Under "Precopulatory Display" of the male Redwing (p. 20) it is said that "In the full intensity display the male walks or jumps around as much as terrain and vegetation permit as he approaches the female. . . ." This is incorrect, the statement unfortunately implying some similarity to precopulatory display of the male Yellowhead. The male Redwing walks or runs toward the female and "jumps around" only as necessary to surmount obstacles in his path, thus on a level surface there is no jumping.

Although a "postcopulatory display" was described and illustrated for the Tricolor (p. 20) and was used as a basis for comparative study, the authors note that there was "insufficient evidence to determine whether this is a regular display which is widely used in this context. . . ." "Postcopulatory display" in the male Yellowhead (illustration based on a photo supplied by me) in which the male raises its tail is said (p. 20) to be of "regular" occurrence. This is misleading. Although tail raising occurs regularly in this species in agonistic situations it does not regularly follow copulation. The statement that "tail raising has not been noted. . . under any circumstances in the Redwing

(except rarely in the Crouch). . ." is also misleading for it is of common occurrence in feeding groups (see Nero, 1956: 13; 1963: 394). No mention is made of the extensive though perhaps inconclusive discussion of tail raising as an appeasement display (in Nero, 1963: 391-394), the authors concluding only (p. 20) that "its function is still obscure."

Considering that this study concentrates on relationships between plumage and communication the statement (p. 5) that the male Yellowhead "apparently has no plumage modifications other than the development of a yellow head and white areas on the wing" is surprising. The yellow cloacal patch (referred to elsewhere by the authors, pp. 20, 72) appears to function in display, and the black area surrounding the eye and the base of the bill may well be significant.

I am credited by the authors as having shown that "Bright colors on the throat and breast are the most common plumage aberrations of the Redwing" (p. 71). This is incorrect. Various albinistic features are far more common. When melanic pigmentation is inhibited in the throat and breast feathers, underlying carotenoid pigments become visible.

Redwings and Yellowheads are said (p. 73) to be "completely dominant to the females at all times"; but, as already pointed out, there are conditions under which male Yellowheads are repulsed by their mates (Nero, 1963: 404).

The statement that "Nero (1963). . . interprets the Asymmetrical Song Spread as a low intensity form of the Symmetrical Song Spread" (p. 16) is an error on the part of the authors (see Nero, 1963: 377).

A great deal of emphasis is given to "Bill-up Flight" of the Yellowhead (pp. 9, 19, 49, 52, for example) which is here regarded as a unique feature of this species. Unfortunately, no comment is made regarding the proposed relationship of "Bill-up Flight" as a homologue of "Bill-up" display (Nero, 1963: 382-386). On the contrary, "Bill-up" display is considered a counterpart of "Bill-down" posture (p. 49). It is even stated (p. 9) that Bill-up Flight may be given with the bill pointed down!

In the Summary (p. 77) a further comparison is drawn between Bill-up Flight of the Yellowhead and territorial flight display in the Redwing and Tricolor, though these are not related displays.

The statement that Yellowheads make "short Bill-up Flights during which the birds also present their backs to each other" (p. 19) is hard to reconcile with males approaching each other in territorial boundary disputes.

Bill-up display in the Redwing female is said (p. 19) to be given "only to other females," though I have already reported it as being given "occasionally to first-year males, and rarely to adult males" (Nero, 1956: 12).

The above are examples of material in this paper that I found erroneous, questionable, or misleading. Possibly an attempt to describe and compare the behavior of three species in 10 pages led to the oversimplification and generalization that in my opinion detract from the value of the section on displays. Moreover, and unfortunately, many of these same points are raised again in the concluding sections of the paper.

Doubtless the main points of the paper regarding the influence of social organization upon the evolution of behavior of these three blackbird species, as suggested to me by Professor Orians in recent correspondence, are valid in spite of my contention that some portions were hastily assembled. Thus the paper attains its major objectives.—ROBERT W. NERO.

A BIRD-BANDER'S GUIDE TO DETERMINATION OF AGE AND SEX OF SELECTED SPECIES. By Merrill Wood. College of Agriculture, The Pennsylvania State University, University Park, 1969: 8½ × 11 in., spiral binding, leatherette covers, 181 pp., 2 figs. \$3.00.

Bird-banders and other field researchers have long felt the need for a guide, summarizing in a single volume, much of what is known about age and sex determination in living birds; Wood's guide is intended as a step in this direction. As the title denotes, however, the book is limited to selected species (I count 160), and coverage is restricted to the northeastern United States. Included are most of the commonly banded Passeriformes (House Sparrow, Blue Grosbeak and House Finch are missing); woodpeckers, a few hawks, small owls, etc. No herons, waterfowl, shorebirds (excepting American Woodcock), gallinaceous birds, gulls, or terns are treated. Also missing are several western and northern species that occur fairly commonly within the northeastern U. S. (Western Meadowlark, Oregon Junco, Gray Jay, Boreal Chickadee, etc.)

The author's approach, based largely on the literature, is in the form of a key. A short introduction covers the "parts" (topography) of a bird. A crude diagram of a spread wing shows 10 secondaries and 10 primaries, with no mention of variation in these numbers, although correct numbering of primaries is essential to the use of wing formulas cited later in the book. Also in the introduction are discussions on the use of the incubation patch and cloacal protuberance in sex determination, and of the "skulling" technique. An index of species treated (pp. 15-16) would be more convenient at the end of the book.

Each bird is listed under its common name, followed by the recommended band size, A.O.U. number, and a statement regarding the reliability of the skulling method for that species. The main section of each key is based on whatever characteristics have been selected to aid in determination of age and sex, and the appropriate code for use in preparing the Federal banding schedules is also indicated. A short summary of molt sequence, usually adapted from Forbush (*Birds of Massachusetts and Other New England States, 1925-1929*) or Roberts (*Manual for the Identification of the Birds of Minnesota and Neighboring States, 1955*), ends each account.

As this work will undoubtedly become the standard guide for hundreds of eastern banders, it is unfortunate that a number of errors and confusions are included. For example, both sexes of the Blue-gray Gnatcatcher in first fall [basic] plumage lack the narrow black line bordering the front part of the crown, which is acquired by the male in a [prealternate I] molt in February. Adherence to Wood's key, however, would classify *any* autumn gnatcatcher lacking the black forehead as a female; in actual practice only the adult male is identifiable after mid-August. In quoting Blake (*Bird-Banding, 27:185, 1956*) on the relative length of the ninth primary of Connecticut and Mourning Warblers, an error is perpetuated that dates back to Ridgway (*U. S. Natl. Mus. Bull., 50, part 2:622, 1902*). The 9th primary of the Connecticut is longer (not shorter) than the 6th, and the 9th primary of the Mourning Warbler is usually shorter (not longer) than the 6th. For a full discussion, see Lanyon and Bull (*Bird-Banding, 38:187-194, 1967*), a paper that should have been in Wood's bibliography. The key for the American Redstart does not allow for males in second year plumage, and after the description of the fully adult male, a correction is needed to allow for birds in this plumage to be designated as ASY (after second year) from January through May; then AHY (after hatching year) only during the autumn months.

Considerable confusion under the Scarlet Tanager is apparently based on a misunderstanding of the timing of the "prebreeding" [prealternate] molt as based on

Forbush (*ibid.*); the age of a spring male cannot be correctly determined as the key is constructed. (From April through June the body plumage of *all* males is scarlet. Birds with gray-brown primaries and secondaries contrasting with black secondary coverts can be classified as second year birds; black primaries and secondary coverts indicate after second year.) The key to the Common Redpoll is also misleading, as it fails to allow for the buffy breasted immature male which does not acquire the pink breast feathers until after the first "postbreeding" [prebasic II] molt. Young males, then, key out as females! Also the bander should regard the key to the Cedar Waxwing as it relates to the red tips of the wing feathers as descriptive only of a general tendency. In the banding of over 3,000 waxwings in southwestern Pennsylvania, I have found many exceptions to this key: Birds of the year occasionally *are* found with very well developed appendages; some older waxwings apparently never acquire them.

The instances listed above represent only a sample of the errors of omission and commission within the main text. Of less importance are editorial errors such as the failure to list a reference to Baird (1964) in the "Literature Used" section at the end of the book; Amadon, 1966 reads "1965" on page 3, and the reference to Roberts (p. 17) should read 1955, not 1967. A more critical editing might have eliminated such minor errors as well as some of the others mentioned above.

The key provides an idea as to the reliability and time limits of the skulling technique for each species, which is the most original contribution of the book. Wood is wisely conservative in his treatment of the subject. As he notes (p. 13), "The skulling method probably can be used safely on many species at dates later than those given in this Guide." The dates that are provided apparently reflect an approximate period after which it may be impossible to differentiate between adults and young because of completed pneumatization in some of the immature birds; that use of the obviously unossified skull after this point is not impaired is unfortunately not explained.

For over two dozen species, including Catbird, the orioles, all of the blackbirds, many northern finches, and the Song Sparrow, we are told: "Age by skulling unlikely." Since space was not a problem (almost all of the keys occupy less than half of the full page allotted), it would have been extremely helpful had a word or two of explanation been given in each case. Do the skulls of these species not pneumatize the first year? Is the skin of the crown too thick? Too dark? Does the skull of the immature pneumatize too early? As it is we can only speculate on Wood's reasoning. In my own experience (in skulling well over 20,000 birds) I find that in many species where the problem is simply seeing the skull because of a dark or thick skin, an experienced bander can safely classify at least some individuals as hatching year birds with the aid of a good artificial light and proper magnification.

There are several other species, listed by the author as safe to "age" by skulling, that my research has indicated (Leberman and Clench, MS. in preparation) often do not ossify until the second year or even later, and it might be appropriate to indicate them in this review. Included are the *Empidonax* flycatchers (use wing bar color as a double check), the White-breasted Nuthatch (the skulls of some individuals may never fully pneumatize), Barn Swallow, Swainson's Thrush, Red-eyed Vireo (use eye color as a double check), Northern and Louisiana Waterthrushes, Yellow-breasted Chat, Scarlet Tanager, and Indigo Bunting. For most of these, however, the area of unossified skull is usually quite small by the second autumn, and birds showing extensively unpneumatized skulls can be determined as hatching year with reasonable assurance.

Wood warns against using too much water in winter for wetting feathers while

skulling, suggesting that the birds be held until dry. At Powdermill Nature Reserve we avoid this problem by wetting the feathers with alcohol, which evaporates in a few seconds.

A surprising number of the keys provide tables for sex or species determination by use of wing or tail length. Nowhere in the guide, however, is the new bander warned that use of such measurements usually requires great caution and judgment. As anyone who has measured the wings of a large sample of birds in the field is aware, the potential of error and inconsistency in his own data, as well as the variability in the methods of others, is great. Positioning of the wing along the rule, the amount of pressure applied, and feather wear all combine to open such measurements to question. Tail measurements on a squirming chickadee are doubly difficult; data for separating such birds as the Carolina and Black-capped Chickadees should, I believe, probably be used only in combination with the slight plumage differences. The geographic variation within such plastic and migratory species as Robin, Slate-colored Junco, and Song Sparrow also adds to the possibility of error in determining sex by wing length; in the Slate-colored Junco, might a large female *J. h. carolinensis* not key out as a male *J. h. hyemalis*?

Caution would seem to be the key to the use of this book, which, despite some inadequacies, will prove useful to the prudent bird-bander. Perhaps its greatest contribution is to point to the gaps in our knowledge and hopefully prompt others to publish their findings. For as Wood notes in his Preface (p. 3), "For any particular species, somewhere there is certain to be a bander who has more information than is presented here. It is hoped that this knowledge will soon become available to others."—
ROBERT C. LEBERMAN.

FROM LAUREL HILL TO SILER'S BOG. THE WALKING ADVENTURES OF A NATURALIST. By John K. Terres. Alfred A. Knopf, 1969. $8\frac{1}{2} \times 6\frac{1}{4}$, xix + 227 pp., 1 map, 32 illus. by Charles L. Ripper. \$6.95.

Obviously John Terres belongs to the modest but select company of naturalists whose chief attributes in the research of natural history consist of time unlimited, spent within one limited area over a long period of years. The results of this kind of research are often astonishing. Reading directly from nature, the keen observer is able to follow installment after installment of events, which he can finally put together to form a factual and significant account. The enchantment and exhilaration of the discoverer is forever the reward of his painstaking work.

All this is contained in Terres' book and for this reason it is not just a tale of rambling roving explorations and haphazard walks in the woods. Ambition and definite aims dictated and directed the naturalist's observations. Concentration counts. The night was often turned into the most intensive work period and the ingeniously devised method and approach brought out meaningful information.

Within the light and poetic framework commenting on the four seasons, study after study disclose facts about rabbits, foxes, mice, flying squirrels, raccoons, birds. We learn how the Turkey Vulture (*Cathartes aura*) is guided to its prey, about the Red-tailed Hawk's (*Buteo jamaicensis*) courtship flights, the Barred Owl's (*Strix varia*) occasional excursions into shallow creeks, catching fish, and the courtship feeding of the Bobwhite (*Colinus virginianus*).

Especially interesting and noteworthy are the rather frequent accounts dealing with predation. The natural ending of a wild life is seldom witnessed, but the patient and

consistent watcher can sometimes follow the concluding episode or piece it together from signs written in the snow and on the ground. A Red-tailed Hawk attempts to strike a Turkey (*Meleagris gallopavo*) with a brood of young, but the ten-pound hen rises into the air and forces the three-pound hawk to turn tail. A rabbit cheats a pack of dogs of their prey, while death in the jaws of a weasel catches up with another.

In the last three chapters the author is at his best, not because the style of writing is outstanding, but because the naturalist is in his glory and his involvement is so complete that it is impossible for the reader not to be carried away with him. A book full of so many attractively presented facts belongs in any nature library worthy of the name. Ripper's sensitive and accurate drawings are a fine asset.—LOUISE DE KIRILINE LAWRENCE.

OWL. By William Service. Alfred A. Knopf, New York, 1969: 5 × 8 in., 93 pp., illus. with drawings by Walter Richards. \$4.00.

This might be called "just one more story of a pet owl"—but it is better than most. At least it was more appealing to this critic, perhaps because the author recognizes anthropomorphism for what it is and is rarely guilty of it, perhaps because of a rather unique style of presentation of his story. Mr. Service speculates on many aspects of Owl's behavior. He performs simple experiments with this bird, described what the bird did, and rarely fell into the trap of attempted interpretation of this behavior. Whether you like owls or not, you will like this appealing little creature.

There is one serious omission. At no time does the author bring out the point that in many states it is illegal to have a Screech Owl in captivity. I find myself shuddering over the number that may be taken into homes now, in misguided attempts to raise a pet like Mr. Service's owl, without permit and without sufficient knowledge of how to do it.—SALLY H. SPOFFORD.

ANNOUNCEMENT

The North American Nest Record Card Program, Laboratory of Ornithology, Cornell University wishes to remind contributors that 1969 nest records are still welcome. In addition the Program desires to accumulate data on nests from the pre-mid-1940s (pre-pesticide era) for comparison. The Program still lacks Regional Centers in Idaho, New Hampshire, New Jersey, and Wyoming.

PROCEEDINGS OF THE FIFTY-FIRST ANNUAL MEETING

JEFF SWINEBROAD, SECRETARY

The Fifty-first Annual Meeting of the Wilson Ornithological Society was held jointly with the Cooper Ornithological Society 18-21 June, 1970, at Colorado State University, Fort Collins, Colorado. Sponsors were Colorado State University, the Colorado Field Ornithologists, the Denver Field Ornithologists, and the Fort Collins Bird Club.

The meeting started on Thursday with a welcome by Gustav A. Swanson, Colorado State University and responses by Robert T. Orr, President of the Cooper Ornithological Society and William W. H. Gunn, President of the Wilson Ornithological Society.

Paper sessions were held Thursday, Friday, and Saturday. On Friday there was a special symposium, Avian Ecology in Grasslands, arranged by John A. Wiens. Friday evening there was a joint informal banquet, a buffalo barbecue and rodeo at the Two-Bar-Seven Ranch. The Colorado Field Ornithologists held a dinner meeting on Saturday.

An evening program on field trips was given Saturday evening by Clait Braun, Birds of Rocky Mountain National Park, and Ronald A. Ryder, Birds of Pawnee National Grasslands.

Three field trips were conducted on Sunday, two all day trips to the aforementioned areas, and a third trip of a half day to local areas.

The recipient of the Wilson Prize, for the best paper presented by a student or non-professional member of the Wilson Society, was announced at the second business meeting and was Ronald M. Case whose paper was "Bioenergetics of a Covey of Bobwhite Quail."

FIRST BUSINESS MEETING

The first business meeting, held Friday morning, was presided over by President Gunn. The minutes of the previous meeting as included in the Proceedings of the Fiftieth Annual Meeting in the Bulletin were approved as published.

The President designated the following temporary committees:

Nominating: Phillips B. Street, Chairman, Aaron Bagg, Olin Sewall Pettingill.

Resolutions: Kenneth C. Parkes, Chairman, Roland C. Clement, W. John Richardson.

Wilson Prize: Harvey I. Fisher, Chairman, Robert W. Storer, Stephen M. Russell.

Auditing: C. Chandler Ross.

The Secretary reported a brief summary of the meeting of the Executive Council of the Society:

1. The Council received and approved reports of the Treasurer, the Trustee's report, the reports of the Membership, Student Membership, Library, Research Committees, and the Editor's report and the Secretary's report.
2. On recommendation of the Research Committee the Council voted to award the Fuertes Award of \$200 to Thomas C. Dunstan, South Dakota University, for his post-fledgling ecology of Great Horned Owls as determined by telemetry.
3. The Membership Committee (David F. Parmelee, Chairman) reported over 100 new members. The President appointed the First Vice President, Pershing B. Hofslund as Chairman of the Membership Committee for the coming year.
4. The Student Membership Committee canvassed a large number of professors at colleges and universities and received 143 nominations for student memberships. The Council commended Chairman Douglas James for his efforts.
5. Dr. George Hall was reelected unanimously as Editor of the Wilson Bulletin.

6. The Council approved a new dues schedule, starting next year. The dues will be: Active—\$8.00; Sustaining—\$15.00; Life—\$200.00; and Patron—\$500.00. There will be a period when Life Memberships will be available at the current level of \$150.00.
7. The 1971 meeting will be held 22–25 April on Dauphin Island, Alabama, with the Mobile County Bird Club as host.

The Treasurer summarized his report which is included here in full for the record:

Report of the Treasurer for 1969

GENERAL FUND

Balance as shown by last report 31 December 1968 \$ 9,429.79

RECEIPTS

Dues

Active Memberships	\$ 3,019.44
Sustaining Memberships	310.00
Subscriptions to The Wilson Bulletin	2,707.00
Sales of back issues of The Wilson Bulletin	935.40
Interest and dividends on savings and investments	2,997.57
Royalties from microfilming back issues of The Wilson Bulletin	111.15
Total Receipts	<u>\$10,080.56</u>

DISBURSEMENTS

The Wilson Bulletin (Printing & Engraving)	\$12,814.24	
Less contributions from authors	650.25	
and illustration fund	1,000.00	11,163.99
The Wilson Bulletin (Mailing & Maintenance of List)		1,722.88
Editor's expense		235.14
Secretary's expense		39.10
Treasurer's expense		391.17
Foreign discount, bank charge, and transfer fees		10.21
Annual Meeting expense		338.70
Committee expense		19.95
Miscellaneous expense		2.00
International Council for Bird Protection (1969 dues)		25.00
Transfer to Research and Award Funds		240.00
Total Disbursements		<u>\$14,188.14</u>
Excess of Disbursements over Receipts for Year 1969		<u>\$(4,107.58)</u>

GENERAL FUND CASH ACCOUNTS

Checking Account	\$ 1,836.99
Savings Account	3,485.22
Balance in National City Bank, Cleveland, Ohio, 31 December 1969	<u>\$ 5,322.21</u>

JOSSELYN VAN TYNE MEMORIAL LIBRARY BOOK FUND

Balance as shown by last report dated 31 December 1968 \$ 156.75

RECEIPTS

Sale of duplicates and gifts	4.50
Total Balance and Receipts	<u>161.25</u>

DISBURSEMENTS

Purchase of Books	33.10
Balance in National City Bank, Cleveland, Ohio, 31 December 1969	\$ 128.15

LOUIS ACASSIZ FUERTES RESEARCH FUND, MARGARET MORSE NICE FUND AND
ANNUAL MEETING PAPER AWARD

Balance as shown by last report dated 31 December 1968	\$ 26.50
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RECEIPTS

Contributions	236.50
Transfer from General Fund	240.00
Total	503.00

DISBURSEMENTS

Award to Richard E. Johnson	\$ 200.00
Award to G. Frederick Shanholtzer	100.00
Award to Martha Whitson	100.00
Total Disbursements	400.00

Balance in National City Bank, Cleveland, Ohio, 31 December 1969	\$ 103.00
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PREPAID STUDENT DUES

Balance as shown by last report dated 31 December 1968	\$ 115.00
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RECEIPTS	0.00
Total	115.00

DISBURSEMENTS	10.00
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Balance in National City Bank, Cleveland, Ohio, 31 December 1969	\$ 105.00
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ENDOWMENT FUND

Balance in Endowment Fund Savings Account as shown by last report dated 31 December 1968	\$ 3,607.00
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RECEIPTS

Life Membership Payments	\$ 1,130.00
Patronship Payments	300.00
Stock Dividends and Exchanges (included below)	
\$5,000 U.S. Treas. 8% notes due 15 May 1971 received in exchange for \$5,000	
U.S. Treas. 4% bonds due 10 October 1969	—
135 shares Phillips Petroleum Co. received from 2 for 1 split	—
33 shares Massachusetts Investors Trust (as capital gains distribution)	—
Total Receipts	1,430.00

DISBURSEMENTS	0.00
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Balance in Endowment Fund Savings Account National City Bank, Cleveland, Ohio, 31 December 1969	\$ 5,037.00
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SECURITIES OWNED (listed at closing prices, 31 December 1969)

United States Government bonds and notes	\$ 9,503.12
Canadian Provincial Government bonds	3,650.00
Corporate bonds	3,400.00

Convertible Corporate bonds	3,750.00
Convertible preferred stocks	21,629.50
Common stocks	14,489.38
Investment trusts	8,080.08
Total Securities Owned	64,502.08
Total Endowment Fund 31 December 1969	<u>\$69,539.08</u>

Respectfully submitted,
WILLIAM A. KLAMM, *Treasurer*

Also for the record here are summaries of the Library Committee's Report and the Editor's Report:

Library Committee (William A. Lunk, Chairman)—There was a considerable increase in the number of contributions and a slight increase in the number of loans and journals received. Four thousand one hundred reprints were a gift of Mrs. Van Tyne from the library of her late husband Josselyn Van Tyne.

Editor's Report (George A. Hall)—Volume 81 (1969) consisted of 496 pages. Papers received today should appear in 15 months. Of major importance to the Bulletin and to the Society was the retirement of Sewall Pettingill from the post as Ornithological Literature Editor. The several editors whom he has served and the Society certainly owe him many thanks for his fine efforts over the years. The new review editor is Dr. Peter Stettenheim.

SECOND BUSINESS MEETING

President Gunn presided over the second business meeting Saturday afternoon. Dr. Kenneth Parkes read the following joint Cooper-Wilson Societies resolutions:

WHEREAS the Cooper Ornithological Society and the Wilson Ornithological Society have assembled in their first joint, annual meeting at Fort Collins, Colorado, 18–21 June, 1970, and

WHEREAS the members of the two societies have benefited greatly from the devoted efforts of the Committee on Arrangements chaired by Dr. Ronald A. Ryder, and

WHEREAS the superior facilities and services provided by Colorado State University have contributed immeasurably to the success and enjoyable nature of this meeting,

THEREFORE BE IT RESOLVED that the Cooper and Wilson Ornithological Societies extend their grateful appreciation to the sponsoring organizations: Colorado State University, The Colorado Field Ornithologists, The Denver Field Ornithologists, and The Fort Collins Bird Club.

WHEREAS the Wilson and Cooper Ornithological Societies represent an important cross section of the scientific community concerned with the study and conservation of birds in North America, and

WHEREAS the officers and members of the Wilson and Cooper Ornithological Societies share a great concern about the future biological productivity of Alaska, particularly in view of pending proposals for exploitation of Alaskan resources,

THEREFORE BE IT RESOLVED that the two societies wish, first, to commend Secretary of the Interior Walter J. Hickel for insisting on proper scientific and engineering assessment of the impact of such exploitation on the environment of Alaska, and, second, to urge that final decisions relating to Alaska be made on the basis of a national accounting rather than merely state, regional, or special interest group considerations, and

BE IT FURTHER RESOLVED that copies of this resolution be sent to Secretary of the Interior Walter J. Hickel and to the Governor, U.S. Senators, and Representatives of the State of Alaska.

WHEREAS more species of endemic birds have become extinct in Hawaii during the past century than in the entire North American continent, and

WHEREAS at least one-third of the extant Hawaiian birds are now classified as "rare and endangered," and

WHEREAS wetland areas are essential to the survival of Hawaii's marsh and pond birds.

THEREFORE BE IT RESOLVED that the Cooper and Wilson Ornithological Societies urge that all State and Federally owned marshlands in Hawaii be declared Wildlife Refuges for these birds, and that pertinent privately owned lands be acquired and put into public ownership by the Federal or State governments or by both, and

BE IT FURTHER RESOLVED that copies of this resolution be sent to Secretary of the Interior Walter J. Hickel and to the Governor, U.S. Senators, and Representatives of the State of Hawaii.

WHEREAS the first joint meeting of the Cooper Ornithological Society and the Wilson Ornithological Society has been a notable success in providing an opportunity for intellectual and social exchange among the members of the societies,

THEREFORE BE IT RESOLVED that the officers of the societies be encouraged to take advantage of every opportunity to stage additional joint meetings of this type at suitable intervals.

Respectfully submitted,

For the Cooper Ornithological Society: Tom J. Cade, Richard F. Johnston,
John Davis, Chairman.

For the Wilson Ornithological Society: W. John Richardson, Roland C.
Clement, Kenneth C. Parkes, Chairman.

The resolutions were approved for both Societies without a dissenting vote by members in attendance at the meeting.

The proposed new members of the Wilson Society as posted were elected without dissenting vote and the Secretary was instructed to cast a unanimous ballot.

The Auditing Committee's report was approved without a dissenting vote. The report included the following statement: "I have examined the Receipts and Expenditure Records of the Wilson Ornithological Society for the period from May 1, 1968 to May 31, 1970. The Receipts Journal was added and the totals verified. Disbursements were verified by examination of checks and bank records. I find all totals in William A. Klamm's records to be correct. And, the balance in the National City Bank of Cleveland Checking Account to be \$5,403.05 as of May 31, 1970. Frank P. McConoughey, Accountant."

The following Nominating Committee's Report was read by Dr. George H. Lowery, Jr.: President, William W. H. Gunn; 1st Vice President, Pershing B. Hofslund; 2nd Vice President, Kenneth C. Parkes; Secretary, Jeff Swinebroad; Treasurer, William A. Klamm; Elective Member of the Council, Elden W. Martin.

The slate was elected and the Secretary was directed to cast a unanimous ballot.

PAPERS SESSIONS

Robert B. Payne, University of Michigan. *Local Song Dialects and Population Size in a Parasitic Bird.*

- George B. Reynard, Cornell University. *Study Problems of some Caribbean Bird Songs.*
- Vivian Telford Anderson, The Utah State University. *The Development of Selected Vocalizations in Hand-reared Black-capped Chickadees.*
- Daniel E. Hatch, University of Nebraska. *Grouping Responses of Wild Quail to Separation Calls of the Bobwhite, Scaled Quail, and their Hybrids.*
- Raymond B. Goldstein, University of Nebraska. *Tracheal Resonance and Vocal Acoustics of some New World Quail.*
- David G. Ainley, Johns Hopkins University. *Comfort Behavior of Adelie, African, and Humboldt Penguins.*
- Sidney A. Gauthreaux, Jr., and Kenneth P. Able, University of Georgia. *The Influence of Wind on the Flight Directions of Passerine Nocturnal Migrants.*
- William E. Southern, Northern Illinois University. *Influence of Disturbances in the Earth's Magnetic Field on Orientation of Ring-billed Gulls.*
- Robert D. Ohmart and Robert C. Lasiewski, University of California, Davis and University of California, Los Angeles. *Energetic Significance of Solar Absorption and Hypothermia in the Roadrunner.*
- Helmut C. Mueller, University of North Carolina. *The Stimuli Eliciting Sunbathing in Birds.*
- Ronald M. Case, Kansas State University. *Bioenergetics of a Covey of Bobwhite Quail.*
- Elden W. Martin, Bowling Green University. *Correlation of Dietary Protein with Energy and Nitrogen Balance, and Temperature Tolerance in Tree Sparrows.*
- Vaughn A. Langman, University of the Pacific. *The development of Radio-biotelemetry Devices for Small Passerine Birds.*
- Cynthia Carey, Occidental College. *Comparison of Salt and Water Regulation in California Quail and Gambel's Quail.*
- Charles H. Trost, Idaho State University. *Cardiovascular Adaptations of Horned Larks to High Altitude.*
- Marsha Landolt and Robert B. Payne, University of Oklahoma. *Thyroid Histology in the Annual Cycle, Breeding, and Molt in Tricolored Blackbirds.*
- Larry C. Holeomb, Creighton University. *Endogenous Factors affecting Incubation Behavior in Red-winged Blackbirds.*
- Nancy S. Mueller, North Carolina State University. *Sexual Dichromatism in the House Sparrow.*
- Charles G. Sibley, Yale University. *Avian Hybridization across the Great Plains.*
- Kendall W. Corbin, Yale University. *Serum Esterase and Lactic Dehydrogenase Polymorphism in the Metallic Starling.*
- Andrew Ferguson, Yale University. *Serum Albumin Polymorphism in *Paradisaea minor*, *Paradisaea raggianna* and their hybrids.*
- Walter J. Bock and John Morony, Columbia University. *Relationships of the Olive Warbler, *Pucedramus taniatus*.*
- Jerome D. Robins and Gary D. Schnell, University of Kansas and O. and S. Ecosystems IRP-IBP. *Skeletal Analysis of the *Ammodramus*-*Ammospiza* Grassland Sparrow Complex: A Numerical Taxonomy Study.*
- Lowell Spring, Oregon College of Education. *A Functional-anatomical Comparison of The Two Murres.*
- George A. Clark, Jr., University of Connecticut. *Bilateral Asymmetry and Individuality of Integumental Patterns on Avian Feet.*
- Robert J. Raikow, University of California, Berkeley. *The Morphology and Phylogenetic Significance of the Pelvic Girdle in Ratites.*

- John Davis, Hastings Reservation, University of California. *Breeding Schedule of the Rufous-collared Sparrow in Coastal Peru.*
- Russel P. Balda and Gary C. Bateman, Northern Arizona University. *Colonial Nesting of the Piñon Jay.*
- Lester L. Short, American Museum of Natural History. *Habits of the Red-fronted Woodpecker, Melanerpes cruentatus.*
- C. John Ralph and Carol A. Pearson, Point Reyes Bird Observatory. *Correlations of Age, Size of Territory, Plumage, and Success in Breeding White-crowned Sparrows.*
- Erwin E. Klaas, Rockhurst College. *Influence of Cowbird Parasitism on Nesting Success in the Eastern Phoebe.*
- Daniel S. McGeen, Oakland University. *Cowbird Density and Cowbird-host Interactions.*
- Bob Stewart, Point Reyes Bird Observatory. *Behavior of Wilson's Warbler.*
- David B. Peakall, Cornell University. *Breeding Biology of the Eastern Bluebird* (read by Tom J. Cade).

Symposium: Avian Ecology in Grasslands,
Chairman: John A. Wiens, Oregon State University

Introductory Remarks by Chairman.

- Ronald A. Ryder, Colorado State University. *Seasonal Fluctuations of Bird Populations on some Colorado Grasslands.*
- William J. Maher, University of Saskatchewan. *Growth Rates of Ground-nesting Passerine Birds at Matador, Saskatchewan, Canada.*
- Paul H. Baldwin, Colorado State University. *Feeding Dynamics of the Lark Bunting.*
- Stephen G. Martin, Oregon State University. *Territorial Quality and Polygyny in the Bobolink.*
- John L. Zimmerman, Kansas State University. *Survival in the Grassland Sere: the Dickcissel's Adaptations for Opportunism.*
- John A. Wiens, Oregon State University. *Habitat Structure and Spatial Relationships among Grassland Birds.*
- Arthur C. Risser, Jr., University of California, Davis. *The Experimental Modification of Starling Reproductive Performance at Different Densities.*
- Keith A. Arnold, Texas A&M University. *Survival of Banded Great-tailed Grackles at College Station, Texas.*
- Vivian R. Null, California State College, Hayward. *Numbers, Species Composition, and Flight Patterns of Gulls near San Francisco Bay, California.*
- Howard L. Cogswell, California State College, Hayward. *Movements of Gulls within and among Local Populations near San Francisco Bay, California.*
- C. W. Comer, Kansas State Teachers College, Emporia. *Winter Activities of the Slate-colored Junco on the Ross Natural History Reservation.*
- David A. Manuwal, University of California, Los Angeles. *Ecology of Cassin's Auklet on Southeast Farallon Island.*
- Eugene Eisenmann, American Museum of Natural History. *Recent Increase and Range Extension of the White-tailed Kite in Middle America.*
- Fred C. Sibley, Point Reyes Bird Observatory. *Annual Nesting of the California Condor.*
- Roland H. Wauer, Big Bend National Park. *Density and Distribution of the Colima Warbler within the Chisos Mountains, Texas.*
- James K. Baker, National Park Service. *The Fluctuating Avifauna of Santa Barbara Island, California.*
- Andrew J. Berger, University of Hawaii. *The Nests and Eggs of some Hawaiian Birds.*

- Richard D. Porter and Stanley N. Wiemeyer, Patuxent Wildlife Research Center. *Reproductive Patterns in Captive American Kestrels.*
- Jay H. Schnell, Tall Timbers Research Station. *A Live-trapping and Recapture Technique for Red-tailed Hawks.*
- Edmund A. Hibbard, North Dakota State University. *Bird Populations of Successional Forest Habitats along the Missouri River in North Dakota.*
- Douglas James and Steven H. Fritts, University of Arkansas. *A Multivariate Analysis of Indigo Bunting Habitat in the Southwestern Part of its Breeding Range.*
- Jed J. Ramsey, Lamar State College of Technology. *Cattle Egrets, Bubulcus ibis, in Southeast Texas.*
- Gene M. Christman, University of California, Berkeley. *Pathologies of Slides at Scientific Meetings.*

Moving Pictures.

- Harvey I. Fisher, Southern Illinois University. *The Laysan Albatross on Midway.*
- C. B. Schaughency, Chester, New Jersey. *Some Birds of Mexico.*
- The Frame House Gallery, Louisville, Kentucky. *A Bird in the Hand—A Bird in the Bush.*

ATTENDANCE

Three hundred twenty nine members and guests were registered. Forty two states, four Canadian provinces and England were represented.

- From **Arkansas**: 3—*Fayetteville*, Douglas A. James; *Little Rock*, Henry N. Halberg, Mrs. Henry N. Halberg.
- From **Arizona**: 4—*Flagstaff*, Russell P. Balda; *Tucson*, Stephen M. Russell, Carl Tomoff, Charles Viers.
- From **California**: 53—*Berkeley*, Gene M. Christman, Jane Durham, James Hunt, Ned K. Johnson, Robert Raikow; *Bolinas*, T. James Lewis, Fred Sibley, Bob Stewart; *Carmel Valley*, John Davis; *Courtland*, Mrs. Arvil Parker; *Davis*, Robert Ohmart, Arthur Risser, Jr.; *Fillmore*, Sidney Peyton; *Hayward*, Howard L. Cogswell, Mrs. Howard L. Cogswell; *Hollywood*, Don Bleitz; *La Jolla*, Miss Grenville Hatch; *La Mesa*, Jean W. Cohn; *Long Beach*, Hal Boley, Charles T. Collins; *Los Angeles*, Cynthia Carey, Nicholas Collias, Elsie Collias, Ed N. Harrison, Lloyd Kiff, Martin Morton, Grace Nixon, Kenneth Stager, Jack C. Von Bloecker, Jr.; *Malibu*, Martine Vozan, Telford H. Work; *Oakland*, Mrs. Enid Austin, Vivian Null; *Orinda*, Tom Schulenberg; *Reseda*, David Manuwal, Mrs. David Manuwal; *Richmond*, Jack Guggoh, Mrs. Jack Guggoh; *Sacramento*, M. D. F. Udvardy; *San Diego*, Gerald Collier, Michael Evans, Marjorie Mason; *San Francisco*, Laurence C. Binford, Robert T. Orr, Edgar Stone; *San Jose*, L. R. Mewaldt, Mrs. L. R. Mewaldt, John Mewaldt; *San Pedro*, Shirley Wells; *Santa Barbara*, Waldo G. Abbott; *Stockton*, M. Dale Arvey; *Twenty-Nine Palms*, James Baker; *Upland*, John Mortensen.
- From **Colorado**: 62—*Aurora*, Lois Webster; *Berthoud*, Mrs. G. T. Cummings, Christian Muller, Mrs. Daniel Muller; *Boulder*, Carl Bock, Mrs. G. M. Booth, William Burt, Gene Elliott, Robbie Elliott, Karlo Hadow, Louise Hering, Mrs. Dorothy A. Herman, Richard Jones, Paul Julian, Mrs. Paul Julian, Terry A. May, David Norris, Mrs. Ralph Odell, Victor Smith, Mrs. Victor Smith, Olwen Williams; *Colorado Springs*, Richard G. Beidleman, Mrs. Nancy Greenleaf, Mrs. Helen Thurlow; *Denver*, Phyliss Caswell, William Eastnian, Thompson Marsh, Mrs. Thompson Marsh, Sadie Morrison, Mary Hope Robins, Miss Tobina Storrie, Donald Thatcher, Lynn Willcockson; *Englewood*, Merle Barbour; *Evergreen*, Winston W. Brockner, Mrs. Winston W. Brockner, Donald Malick; *Fort Collins*, Paul H. Bald-

win, Clait Braun, Terry Colc, Phil Creighton, N. R. French, David Lupton, Wayne Marion, Carl Marti, Meredith Morris, Richard Olendoroff, Gary Packard, Helen Ryder, Raymond Ryder, Ronald A. Ryder, Mrs. Ronald A. Ryder, Gustav A. Swanson; *Grand Junction*, William Davis; *Greeley*, Maynard Stamper; *La Junta*, William Anderson, Babette Cranson, Mrs. Robert Wolfe; *Lakewood*, William Rayall, Jr.; *Longmont*, Allegra Collister; *Loveland*, Jean Christensen, Mr. I. K. Robertson.

From **Connecticut**: 6—*New Haven*, Peter Bottjer, Kendall Corbin, Andrew Ferguson, Charles G. Sibley, Mrs. Charles G. Sibley; *Storrs*, George A. Clark, Jr.

From **District of Columbia**: 3—*Washington*, Richard C. Banks, George E. Watson, Richard L. Zusi.

From **Florida**: 1—*Tallahassee*, Jay Schell.

From **Georgia**: 2—*Athens*, Kenneth P. Able, Sidney A. Gauthreaux, Jr.

From **Hawaii**: 1—*Honolulu*, Andrew J. Berger.

From **Idaho**: 1—*Pocatello*, Charles Trost.

From **Illinois**: 12—*Blue Island*, Karl Bartel; *Carbondale*, Harvey Fisher, Mrs. Harvey Fisher, David Hayward, Vernon Kleen, Hohn Krull; *DeKalb*, William Southern; *Havana*, Frank C. Belrose, Jr.; *Lebanon*, Ernest Willoughby; *Macomb*, Robert Beason, Edwin Franks, Mrs. Edwin Franks.

From **Indiana**: 3—*Hanover*, J. Dan Webster; *Richmond*, C. S. Snow, Mrs. C. S. Snow.

From **Iowa**: 5—*Davenport*, Maria Costa, Peter Peterson, Mrs. Peter Peterson; *Grinnell*, Helen Stewart, Mildred Stewart.

From **Kansas**: 6—*Emporia*, C. W. Comer; *Hays*, Charles Ely; *Lawrence*, Richard F. Johnston, Jerome D. Robins; *Manhattan*, Ronald Case, John L. Zimmerman.

From **Kentucky**: 1—*Richmond*, A. L. Whitt, Jr.

From **Louisiana**: 4—*Baton Rouge*, George H. Lowery, Mrs. George H. Lowery; *Shreveport*, Horace H. Jeter, S. O. Williams III.

From **Maryland**: 9—*Baltimore*, David G. Ainley, C. John Ralph; *Elliott City*, Earl Baysinger, Mrs. Earl Baysinger; *Laurel*, Richard Porter, Chandler Robbins, Mrs. Chandler Robbins, Jeff Swinebroad; *Suitland*, James A. Bruce.

From **Massachusetts**: 6—*Franklin*, John Minot; *Littleton*, James Baird, Robert Baird; *Middleboro*, Paul Anderson, Mrs. Paul Anderson; *South Wellfleet*, Wallace Bailey.

From **Michigan**: 6—*Ann Arbor*, Robert W. Storer, Nancy White; *East Lansing*, George Wallace, Mrs. George Wallace; *Mt. Pleasant*, Harold Mahan; *Pontiac*, Daniel S. McGeen.

From **Minnesota**: 11—*Duluth*, Joel Bronoel, Mrs. Joel Bronoel, P. B. Hofslund; *L-
Moille*, Mrs. Violet Nagle, Mrs. Pauline Wershofen; *Minneapolis*, Walter Breckenridge, Mrs. Walter Breckenridge; *South St. Paul*, Thomas Savage, Mrs. Thomas Savage; *Stillwater*, John Erickson, Mrs. John Erickson.

From **Missouri**: 9—*Columbia*, W. Reid Goforth; *Kansas City*, Erwin Klaas, Mrs. Erwin Klaas; *St. Louis*, Richard A. Anderson, Mrs. Richard A. Anderson, Margaret Feigley, Mrs. Joel Massis, James Mulligan, Lillian Nagel.

From **Nebraska**: 8—*Chadron*, Mary Blinde, Doris Gates; *Lincoln*, Esther Bennett, Calvin Cink, Raymond Goldstein, Daniel Hatch, Alice Prosofski; *Omaha*, Larry Holcomb.

From **New Hampshire**: 1—*Manchester*, Mrs. Robert P. Booth.

From **New Jersey**: 15—*Cape May Point*, Ernest A. Choate; *Chester*, Charles Schaughency, Mrs. Charles Schaughency; *Mountainside*, Albert Schnitzer, Mrs. Albert Schnitzer; *Newfoundland*, Evamarie Townsend; *Orange*, Anne Wachenfeld;

- Princeton*, Charlotte DuBois; *Ramsey*, Mrs. Eleanor Dater; *Riverton*, Kenneth Reynard, Mrs. Kenneth Reynard, George Reynard; *Wenonah*, Edward Manners, Mrs. Edward Manners; *Westfield*, Norman Pilling.
- From **New Mexico**: 2—*Las Cruces*, Donald Caccamise, Ralph J. Raitt.
- From **New York**: 16—*Buffalo*, Alice Ulrich; *Ithaca*, Susan M. Budd, Tom J. Cade, Mrs. Cyril Comar, Charles Leck, Carol Pearson, Olin S. Pettingill, Jr., Mrs. Olin S. Pettingill, Jr., W. John Richardson; *New York City*, Dean Amadon, Mrs. Dean Amadon, Walter Bock, Eugene Eisenmann, Lester L. Short; *Rochester*, Roland C. Clement; *Waterloo*, Jayson Walker.
- From **North Carolina**: 2—*Chapel Hill*, Helmut C. Mueller; *Raleigh*, Nancy Mueller.
- From **North Dakota**: 1—*Fargo*, Edmund A. Hibbard.
- From **Ohio**: 12—*Bowling Green*, Elden W. Martin; *Burton*, Robert McCullough; *Charlodon*, Marjorie Ramisch; *East Liverpool*, John Laitsch, Mrs. John Laitsch; *Gambier*, Robert Burns; *Lakewood*, William A. Klamm, Mrs. William A. Klamm; *Oxford*, David R. Osborne; *Painesville*, Mrs. Robert Booth; *Ravenna*, Mildred Daniels, Estrilla Daniels.
- From **Oklahoma**: 2—*Norman*, Marsha Landolt, Robert B. Payne.
- From **Oregon**: 7—*Ashland*, John O. Sullivan; *Burns*, Carroll D. Littlefield; *Corvallis*, Stephen Martin, John Rotenberry, John A. Wiens; *Forest Grove*, Vaughan A. Langman; *Monmouth*, Lowell Spring.
- From **Pennsylvania**: 5—*Chester Springs*, Phillips B. Street; *Newton*, Lester Thomas, Mrs. Lester Thomas; *Philadelphia*, C. Chandler Ross; *Pittsburgh*, Kenneth C. Parkes.
- From **Puerto Rico**: 2—*Palmer*, Cameron B. Kepler, Mrs. Cameron B. Kepler.
- From **South Dakota**: 3—*Rapid City*, L. M. Baylor, Keith Evans, Nathaniel R. Whitney.
- From **Tennessee**: 5—*Elizabethton*, Lee R. Herndon, Mrs. Lee R. Herndon; *Gatlinburg*, Arthur Stupka, Mrs. Arthur Stupka; *Maryville*, Ralph J. Zaenglein.
- From **Texas**: 6—*Austin*, Gary Schnell; *Beaumont*, Jed Ramsey; *Big Bend Natl. Park*, Roland Wauer; *College Station*, K. A. Arnold; *Dallas*, Cecil Kersting; *Huntsville*, Ralph Moldenhauer.
- From **Utah**: 12—*Brigham City*, Michael Long; *Logan*, Vivian Telford Anderson, Dick Burr, K. L. Dixon, Martha Lester, Mike Minoock, Joe Platt, June Rushing, Richard Wilson, Janet Young; *Salt Lake City*, William Behle, Mrs. William Behle.
- From **Virginia**: 2—*Manassas*, Mrs. Roxie Laybourne; *Williamsburg*, Mitchell A. Byrd.
- From **Washington**: 5—*Ellensburg*, F. John Erickson, Donald F. Martin, Jared Verner, Mrs. Jared Verner; *Seattle*, Frank Richardson.
- From **West Virginia**: 3—*Inwood*, Clark Miller; *Morgantown*, George A. Hall, Mrs. George A. Hall.
- From **Wisconsin**: 2—*Madison*, John Watson; *Viroqua*, Margarett Morse.
- From **Wyoming**: 1—*Laramie*, Kenneth Dicm.
- From **Alberta**: 1—*Calgary*, M. J. Myres.
- From **Ontario**: 3—*Aurora*, R. G. Brown; *Newmarket*, Reg E. Chandler, Mrs. Reg E. Chandler; *Toronto*, William W. H. Gunn.
- From **Quebec**: 1—*Montreal*, David Nettleship.
- From **Saskatchewan**: 1—*Saskatoon*, William Maher.
- From **England**: 1—*Manchester*, John Mosher.

Also attending: Larry DeBord, Jimm Gessaman, Douglas Vogelcer.

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CONTENTS

- MALES IN BREEDING PLUMAGE OF THE RACES OF THE *DENDROICA*
CORONATA COMPLEX, Watercolor by *Theodore R. Miley* facing page 355
- GEOGRAPHIC VARIATION IN THE *DENDROICA CORONATA* COMPLEX
John P. Hubbard 355
- NESTING BIRD ECOLOGY OF FOUR PLANT COMMUNITIES IN THE
MISSOURI RIVER BREAKS, MONTANA *Kenneth C. Walcheck* 370
- OLDSQUAWS NESTING IN ASSOCIATION WITH ARCTIC TERNS AT
CHURCHILL, MANITOBA *Roger M. Evans* 383
- SEASONAL CHANGES IN FLOCKING BEHAVIOR OF STARLINGS AS
CORRELATED WITH GONADAL DEVELOPMENT *G. James Davis* 391
- SPATIAL DISORIENTATION IN BIRDS *A. D. Herbert* 400
- BREEDING POPULATIONS OF TULE WHITE-FRONTED GEESE IN
NORTHWESTERN ALASKA *Bob Elgas* 420
- WINTER DOMINANCE RELATIONSHIP IN BLACK-CAPPED CHICKADEES
Jonathan E. Hartzler 427
- A COMPARATIVE STUDY OF NESTING FORSTER'S AND BLACK TERNS
Robert D. Bergman, Peter Swain, and Milton W. Weller 435
- BREEDING BIOLOGY OF AMERICAN COOTS IN IOWA
Leigh H. Fredrickson 445
- NESTING SUCCESS AND MORTALITY OF NESTLINGS IN A
CATTLE EGRET COLONY *Julian L. Dusi and Rosemary T. Dusi* 458
- GENERAL NOTES
- MALLARD-GREEN-WINGED TEAL ASSOCIATIONS IN SOUTHERN WISCONSIN
Carl H. Nellis, James J. Zohrer, and Daniel W. Anderson 461
- A SECOND SWALLOW-TAILED KITE RECORD FOR TRANS-PECOS TEXAS
Roland W. Wauer 462

GIANT WATERBUG IN AN OWL PELLET	<i>Walter Kingsley Taylor</i>	462
EGG TRANSPORT RECORDED FOR THE RED-BELLIED WOODPECKER		
	<i>Graham C. Hickman</i>	463
EASTERN PHOEBE NESTING IN OLD BARN SWALLOW NEST ...	<i>Harmon P. Weeks, Jr.</i>	463
HERMIT WARBLER IN MISSOURI	<i>David A. Easterla</i>	464
YELLOWTHROAT CAUGHT IN COMMON BURDOCK	<i>Richard D. Brown</i>	464
THE DOUBLE-SCRATCH IN THE GENUS <i>POOECETES</i>	<i>Walter Kingsley Taylor</i>	465
COMMON CRACKLE KILLS CEDAR WAXWING IN AIR	<i>Erma J. Fisk</i>	465
FIRST NESTING COLONIES OF THE LARK BUNTING IN MISSOURI		
	<i>David A. Easterla</i>	465
ORNITHOLOGICAL NEWS		467
ORNITHOLOGICAL LITERATURE		469
Lorus and Margery Milne, <i>Birds of North America</i> , reviewed by Olin Sewall Pettingill, Jr.; Robert H. Giles, Jr., editor, <i>Wildlife Management Techniques</i> , reviewed by D. A. Lancaster; Theed Pearse, <i>Birds of the Early Explorers in the Northern Pacific</i> , reviewed by Warren B. King; J. A. Baker, <i>The Hill of Summer</i> , reviewed by Louise deK. Lawrence; Helmut K. Buechner and Jimmie H. Buechner, editors, <i>The Avifauna of Northern Latin America</i> , reviewed by George A. Hall.		
THE WILSON ORNITHOLOGICAL SOCIETY, OFFICERS AND COMMITTEE		
CHAIRMAN		474
INDEX TO VOLUME 82, 1970		475
MEMBERSHIP LIST (Supplement to Vol. 82, No. 4)		



T. Miley

Males in breeding plumage of the races of the *Dendroica coronata* complex (from top): *D. c. coronata*, *D. c. auduboni*, *D. c. nigrifrons*, *D. c. goldmani*. Watercolor by Theodore R. Miley.

GEOGRAPHIC VARIATION IN THE *DENDROICA CORONATA* COMPLEX

JOHN P. HUBBARD

THE *Dendroica coronata* (L.) complex consists of the Myrtle Warbler (*D. coronata*), which breeds in the boreal forests of North America, and Audubon's Warbler (*D. auduboni* Townsend), which breeds in the forests of western North America. Although the two are generally regarded as distinct species, they intergrade in southwestern Canada and should be considered as a conspecies, or better, as two semispecies (Hubbard, 1969). Besides the nominate forms, one other has been named in the Myrtle group (i.e., *hooveri* McGregor) and three in the Audubon group (i.e., *memorabilis* Oberholser, *nigrifrons* Brewster, and *goldmani* Nelson). The last revisions were by Godfrey (1951) in the *coronata* group and by Oberholser (1921) in the *auduboni* group.

The present paper is the outgrowth of a comprehensive analysis of geographic and other types of variation (Hubbard, 1967), which was done prior to study of the interbreeding of the two semispecies groups (Hubbard, 1969). My object here is to describe salient features of the geographic variation in each of these groups and to assess the named forms (no new forms are proposed). For a more detailed review of variation in this complex the reader is referred to my 1967 work, available from University Microfilms, Ann Arbor, Michigan.

In extending formal, subspecific recognition to populations I followed the suggested criteria of Mayr et al. (1953), in accepting as valid those entities that are separable *inter se* on a 75 per cent from a near 100 per cent (or 90 from 90 per cent) basis. A further requirement is that the probability of correct segregation within a random sample be 95 per cent or better. While recognizing the need for certain minimum and arbitrary standards in the application of formal names to populations, I also feel that in some cases what might be termed "infra-subspecific" variation can be usefully singled out. For example, by being able to identify distinctive extremes that characterize certain populations one may gather information on dispersal, molt cycles, and other aspects of the biology even though the populations in question are not "good" subspecies. Such infra-subspecific entities can be designated by breeding range rather than by a formal name and thus provide the practical benefits of the subspecies concept without further burdening scientific nomenclature.

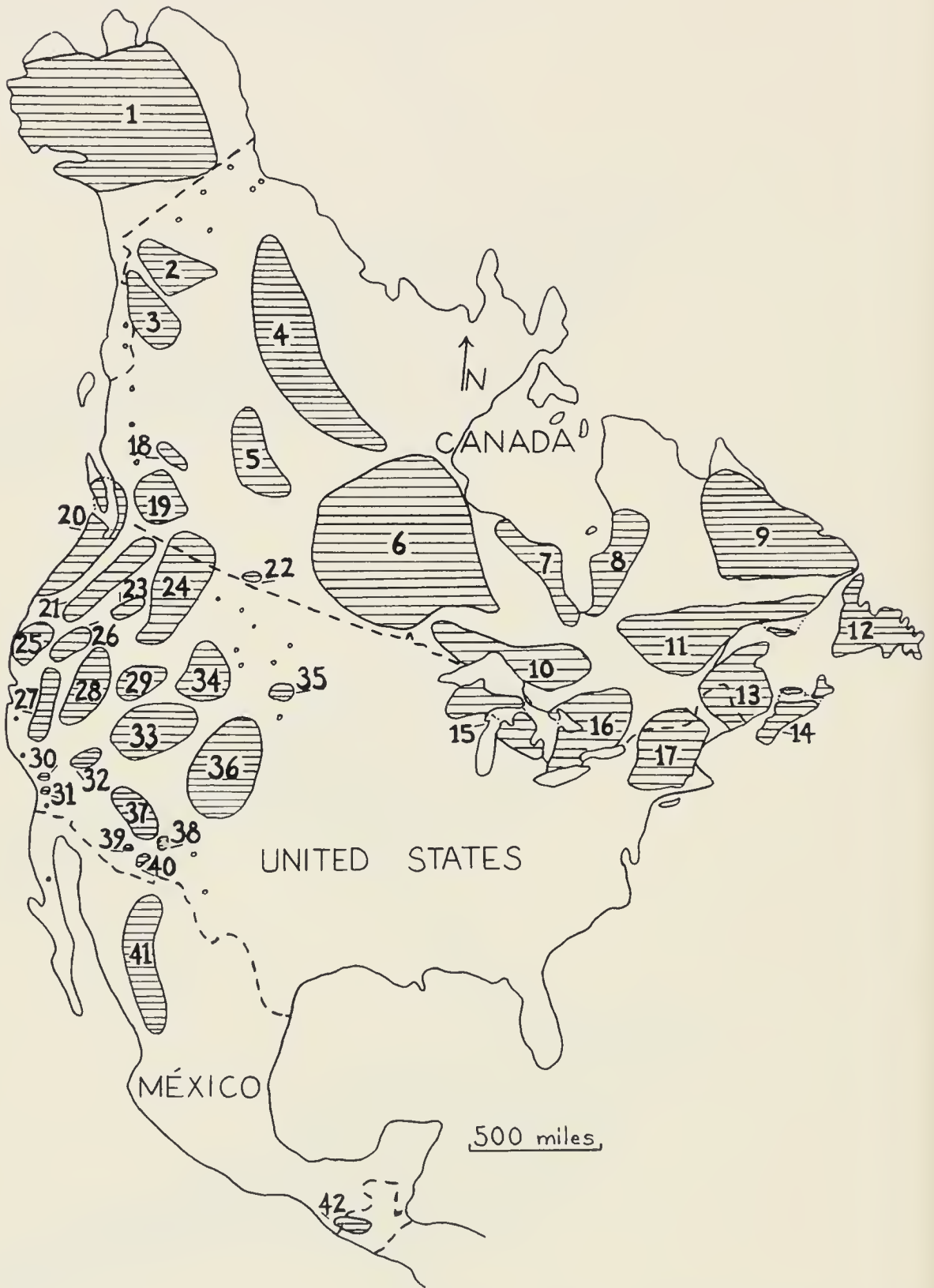


FIG. 1. Geographic samples used in analysis of mensural characters in the *Dendroica coronata* complex. Numbers 1 through 17 are *coronata* group and 18 through 42 the *auduboni* group (nominal designations of numbers in TABLE 1).

MATERIALS AND METHODS

This study is based on 350 specimens in winter plumage, 563 juveniles (none available of *goldmani*), and 2,069 specimens taken in the breeding season. The breeding season is arbitrarily considered to be 1 June (15 May in the Pacific Northwest and northernmost North America) through the time of the end of the postnuptial molt and applies to specimens taken in suitable breeding areas. For various analyses specimens were segregated into juveniles (includes both sexes), first-year males (i.e., males that have completed the postjuvinal but not the first postnuptial molt), adult males (i.e., males that have completed at least one postnuptial molt), and females. First-year males were found to be about 90 per cent separable from adults on the basis of their generally browner (and more worn) remiges, rectrices, and especially primary coverts and alular feathers (verified by juveniles and skull-aged specimens); adults have these feathers more blackish, often with grayish edgings, and less worn. Although similar differences exist in females, the segregation of age classes was not attempted because the differences are much more subtle and less consistent.

Breeding specimens within each of the two semispecies were segregated into the smallest geographic samples possible for a preliminary multivariate analysis of linear measurements, with subsequent recombination of certain samples to better study and present the data (Fig. 1). Linear measurements used were lengths of wing (chord), tail, culmen (nostril to tip), and tarsus, all but the last using established methods. The tarsus was measured from the posterior depression of the tibio-metatarsus joint to the proximal base of the hallux, *provided* that the latter was positioned 90 ± 45 degrees relative to the tarsometatarsus (positions outside that range were found to alter tarsus length by 1 to 2 mm). In spite of these qualifications most specimens were measurable for tarsus length, and this method of measurement was found to be faster than and as accurate as the traditional one. Wing and tail length were found to be strongly correlated, and as a result only wing length was used in the mensural analysis on an absolute basis.

Body weight of breeding males was also used to compare samples, those of females being excluded as too variable due to variation in weight of gonads and gonadal products (Hubbard, 1967). Body weight was found to vary independently of the linear measurements used above and is treated separately.

The amount of white in each rectrix was scored as follows: a very small spot or narrow marginal edging (0.125); a small spot or narrow marginal blotch (0.25); a medium spot or small marginal blotch (0.5); a large spot or medium marginal blotch (0.75); or a large marginal blotch (1.00). The values for each pair of rectrices were summed to obtain the score of white in the tail of each specimen and these were used to compare sample means.

Statistical procedures follow Steel and Torrie (1960) and other specified sources. Variances were calculated for samples of six or more specimens, and differences between sample measurements are accepted as significant when at or greater than the 0.05 level of probability.

RESULTS AND DISCUSSION

Coronata Group

This group breeds from New England, eastern New York, southern Ontario, central Michigan, southern Manitoba, southern Saskatchewan, central Alberta, northern British Columbia, and southeastern Alaska northward to tree line (Fig. 1) and is migratory throughout its breeding range. Intergradation with

the *auduboni* group occurs in southeastern Alaska, central and eastern British Columbia, and southwestern Alberta and is discussed elsewhere (Hubbard, 1969).

Within the *coronata* group I found geographic trends in the variation of both color and pattern of plumage and in mensural characters. Plumage characters which vary are extent of black in the breast of breeding males, color and extent of streaking on the upperparts of breeding females, the color of the upperparts of winter-plumage specimens, and extent of white in the outer rectrices. Mensural characters which vary are body weight of breeding males and lengths of tarsus and wing. Purported differences in the hue of the yellow rump (Oberholser, 1918), color of the upperparts of juveniles (Oberholser, 1918; Godfrey, 1951), and of the extent of dorsal streaking in winter plumage (Godfrey, 1951) were not substantiated.

In breeding-plumaged males the black on the breast varies from streaking to solid, with the former extreme predominating in the northwest (Alaska, Yukon, and British Columbia) and the latter in Labrador-Newfoundland. In northwestern males (81 specimens in 3 samples) 56 to 66 per cent were streak-breasted and the remaining 34 to 44 per cent were mottled with black on the breast. In the Prairie Provinces the streak-breasted type composed 20.5 per cent in a sample of 29 males, while 79.5 per cent were mottle-breasted. Farther east, 10.5 per cent of 151 males were streak-breasted, 74.7 per cent mottle-breasted, and 14.8 per cent solid-breasted, except in Labrador-Newfoundland (14 males) where none was streak-breasted and 50.0 per cent each were mottle- and solid-breasted. From these data two points can be made: one, no geographic area can be characterized by a single breast type; and, two, only solidly black-breasted males are confined to an area discrete enough to be useful in reliably segregating specimens. Thus, solid-breasted males may be said to originate in eastern North America, east of the Prairie Provinces, with a confidence level of 100 per cent. In my sample of males some 15.0 per cent are of this type and can thus be assigned geographically on this character.

In breeding-plumaged females the upperparts vary from light brown (occiput light gray) with light streaking to dark brown with heavy streaking: the light brown type predominates in the west and the dark brown in the east. In northwestern females (39 specimens in 3 samples) the light brown type composed 72.7 to 76.5 per cent, while zero to 5.0 per cent were dark brown and 22.3 to 23.5 per cent were intermediate. In Alberta the light brown type constituted 68.0 per cent of 25 specimens and 32.0 per cent were intermediate. Farther east the light brown type was 4.9 to 12.5 per cent (73 specimens in 3 regional samples), while 65.8 to 68.8 per cent were dark brown and 18.7 to 29.3 per cent were intermediate. While most specimens in regional samples

fall into one or the other extreme of this character and show a geographic tendency in the trend of variation, 23.5 to 34.2 per cent of the specimens in each sample fall in the opposite extreme and intermediate categories. This means that no sample or area can be characterized by a single plumage type. Furthermore, of the two extremes only the dark brown type is sufficiently limited in its distribution and frequency to be useful in reliable segregation of specimens. Thus, females with dark brown, broadly streaked upperparts may be attributed to North America, east of Alberta; in my samples the confidence level of this segregation is 97 per cent, and 37 per cent of female specimens may be identified in this way.

In the color of the upperparts winter-plumaged specimens vary from light to dark brown, with or without a rufescent wash. Study of this character is made difficult because of the problem of obtaining winter specimens from known breeding areas. In my analysis I used 40 specimens taken in late summer and autumn, and segregated by sex and age classes, from Alaska and northwestern British Columbia, compared to 80 from southeastern Canada and the adjacent United States. In the northwestern sample 92.5 per cent of the specimens fell into the categories of light, rufescent brown or dark brown, while the remaining 7.5 per cent were either light brown or dark, rufescent brown. By comparison 68.7 per cent of the eastern specimens fell into the first two categories (i.e., light, rufescent brown and dark brown), whereas 12.5 per cent were light brown and 18.8 per cent were dark, rufescent brown. These comparisons show different frequencies of color types between the two samples, but complete overlap exists among the types. The degree of overlap is such that reliable segregation of specimens on a geographic basis is not possible.

The final plumage character in which I found geographic variation is the amount of white in the outer rectrices, with the average scores in northwestern populations being higher than those in more easterly ones. In adult males from Alaska, the Yukon, British Columbia, and MacKenzie the values are 3.2 to 3.6, compared to 3.0 to 3.1 in more eastern samples. In first-year males from the northwestern area the values are 2.7 to 3.2 compared to 2.5 to 2.7 eastward except for 2.9 on the western side of Hudson Bay. In females the northwestern values (excluding MacKenzie which is 2.5) range from 2.7 to 2.8, compared with 2.4 to 2.6 eastward except for 2.8 in southern Manitoba. The differences are relatively minor and overlap occurs in means of first-year males and females, as well as in individuals of all samples. Further, some inconsistency exists in the area from MacKenzie to Hudson Bay, perhaps due to introgression with *auduboni*. Thus, in spite of trends in average differences no effective separation of populations is possible on the basis of this character.

TABLE I

WING LENGTH (MM) IN BREEDING SAMPLES OF THE *DENDROICA CORONATA* COMPLEX

Semispecies groups Sample	Adult males			First-year males			Females		
	no.	mean	S.D.	no.	mean	S.D.	no.	mean	S.D.
<i>Coronata</i> group									
1. Alaska	14	77.1	1.8	23	75.3	1.3	16	72.9	1.1
2. Yukon	13	76.5	1.6	12	74.5	1.3	9	72.3	0.9
3. Northwest British Columbia ¹	13	76.8	1.1	24	75.0	1.4	27	71.4	1.2
4. MacKenzie	9	74.7	0.8	7	72.7	0.8	9	69.7	1.1
5. Central Alberta ¹	8	74.1	1.6	9	72.4	1.7	9	69.0	1.8
6. Manitoba	5	73.0	—	12	72.0	1.6	11	68.4	1.7
7. West James Bay	9	74.3	1.7	7	72.5	1.3	8	69.3	0.9
8. East James Bay	6	74.9	1.5	11	71.8	0.9	14	69.3	1.5
9. Labrador	12	74.5	1.5	4	71.8	—	12	69.7	1.4
10. Central Ontario	11	73.9	1.7	15	71.7	1.4	16	69.0	2.4
11. Quebec	9	74.0	1.2	19	72.6	1.2	16	69.3	1.1
12. Newfoundland	6	74.7	2.4	8	72.5	1.6	10	70.1	2.3
13. New Brunswick	5	73.0	—	12	71.3	0.9	13	68.7	1.5
14. Nova Scotia	9	74.1	2.0	10	72.4	1.2	10	67.9	1.3
15. Michigan	12	73.0	1.0	20	71.7	1.7	9	68.3	0.7
16. Southeast Ontario	11	73.3	1.5	10	71.6	2.0	8	68.3	1.0
17. Northeast United States	7	74.1	1.3	15	72.1	1.9	13	68.6	1.3
<i>Auduboni</i> group									
18. Central British Columbia ²	10	76.5	1.3	15	74.5	1.6	2	72.6	—
19. Southern British Columbia	8	77.7	1.4	12	75.2	1.3	18	71.6	1.6
20. Northwest Coast	13	76.6	1.3	21	74.0	1.4	24	71.4	1.4
21. Cascades	13	78.0	1.6	17	75.1	1.4	12	73.3	1.6
22. Cypress Hills	6	78.0	1.3	7	77.3	1.4	11	73.5	1.7
23. Northeast Oregon	14	77.9	1.6	10	76.3	1.2	7	73.8	0.8
24. Idaho	7	79.4	1.6	18	75.9	1.5	22	73.3	1.0
25. Northwest California	12	79.0	1.5	14	76.4	1.9	17	73.9	1.3
26. Northeast California	14	79.6	1.9	17	76.4	1.1	10	73.4	1.9
27. Sierra Nevada	30	79.7	1.5	41	77.1	1.8	47	74.4	1.8
28. Western Nevada	13	80.3	1.8	9	76.8	0.8	8	74.8	1.6
29. Northeast Nevada	7	80.5	2.3	10	77.1	1.6	12	74.4	1.6
30. San Bernardino Mts.	17	79.7	1.3	12	78.0	2.1	10	74.3	1.8
31. San Jacinto Mts.	7	80.0	1.3	7	76.5	1.2	12	76.6	1.4
32. Southern Nevada	8	80.0	1.4	8	77.8	1.7	10	73.5	1.8
33. Utah	14	80.3	1.2	19	77.5	1.3	15	74.3	2.0
34. Northwest Wyoming	14	80.2	1.2	16	77.6	1.4	27	74.6	1.5
35. Black Hills	17	81.4	0.5	8	78.6	1.0	13	76.5	1.4
36. Southern Rockies	31	80.7	1.8	22	77.9	1.2	20	75.1	1.6
37. Central Arizona	15	80.7	1.3	12	78.8	1.1	11	76.0	1.8
38. Mogollon Mts.	11	80.8	1.9	9	78.9	1.4	10	75.4	1.5

¹ Intergrades toward *auduboni*.² Intergrades toward *coronata*.

TABLE 1 (Cont'd.)

Semispecies groups Sample	Adult males			First-year males			Females		
	no.	mean	S.D.	no.	mean	S.D.	no.	mean	S.D.
<i>Auduboni</i> group (Continued)									
39. Santa Catalina Mts.	18	81.8	1.7	27	79.5	1.4	19	76.4	1.8
40. Chiricahua Mts.	10	81.1	0.6	9	79.3	1.8	10	77.3	1.4
41. Sierra Madre Occidental	35	83.0	2.4	20	80.0	1.2	24	77.8	2.2
42. Chiapas-Guatemala ³	9	84.4	1.6	6	81.3	1.5	11	78.9	1.5

³ Includes specimens taken throughout the year.

Mensural variation.—In analyzing body weights I was hampered by the lack of data, and conclusions are necessarily tentative. In comparisons of the only two sizable samples, I found a significant difference to exist between the means of eight males from Alaska (weight 13.5 ± 0.7 grams) and that of 13 from Michigan (weight 11.8 ± 0.4 grams). Among the few other weights available, those from Ontario and the northeastern United States were similar to the Michigan series and those from the Yukon and northwestern British Columbia were similar to the Alaskan ones. However, three weights from Quebec are intermediate (range 12.4 to 13.1 grams), which may suggest that weight increases from south to north rather than just northwestward. Obviously more data are needed to properly assess this character.

For the tarsus a slight increase in mean length occurs from southern Canada and the adjacent United States northward to Labrador-Newfoundland on the east and Alaska-Yukon-British Columbia on the west, although locally the variation becomes mosaic rather than geographic in distribution. The means in southern areas are 16.9 to 17.7 mm in males compared to 17.5 to 18.1 mm in the northwest and 17.9 to 18.2 mm in Labrador-Newfoundland (females average smaller in size but show parallel trends). No reliable segregation of populations is possible on the basis of this measurement because of overlap and the slight differences involved.

One finds that wing lengths of populations from the northwest (Alaska, the Yukon, MacKenzie Delta, and northwestern British Columbia) average larger than those to the east (Table 1). In adult males the means are 76.5 to 77.1 mm in the northwest and 73.0 to 74.9 mm to the east; in first-year males 74.5 to 75.3 mm in the northwest, 71.3 to 72.7 mm to the east; and in females 71.4 to 72.9 mm to 67.9 to 70.1 mm.

I compared the group of easterly specimens with that from the northwestern and found that the separability in adult males (east versus northwest) is 70.7 per cent from 20.6 per cent, in first-year males 94.3 per cent from 36.9 per cent, and in females 91.1 per cent from 30.6 per cent. This degree

of separability (confidence level 95 per cent) falls far short of the 75 from ca. 100 per cent (or 90 from 90 per cent) levels suggested by Mayr et al. (1953), and even on a less reliable basis of segregation (confidence level 75 per cent) the maximum separability is still only 89.5 to 83.1 per cent in easterly specimens and 61.7 to 86.1 per cent in the northwestern ones. Obviously separation of populations of wing length is not possible in the *coronata* group on a reliable and large-scale basis.

Summary of variation and nomenclatural conclusions.—This review of geographic variation reveals the existence of several characters in the *coronata* group which reliably distinguish populations (confidence level of 95 per cent or more), including longer wing in northwestern North America, and shorter wing, more extensively black breast in breeding males, and darker brown upperparts with heavier streaking in breeding females in more easterly North America. Other characters show minor differences, overlap, or other factors which negate their value in separation of populations, and include the color of the upperparts in winter plumage, amount of white in the outer rectrices, weight (data incomplete and inconclusive), and tarsus length. The reliable characters, even when combined (on the basis of random association), do not produce a sufficient level of separability to justify subspecific recognition of two populations, i.e., at least 75 per cent from about 100 per cent (or 90 from 90 per cent). In eastern populations the segregation by breeding plumage characters and wing length is 75.5 per cent in adult males, 96.1 per cent in first-year males, and 97.1 per cent in females, compared to 20.6 per cent, 36.9 per cent, and 30.6 per cent in the respective categories in northwestern populations, which are solely separable by wing length. Thus the separation of the latter population as a formal subspecies is unwarranted, and the name *hooveri* (McGregor, 1899) is considered a synonym. Nevertheless, the fact remains that the specified portions of the specimens from the two areas are reliably separable, and as segregation of such specimens may be of value, it is provided for in the key included in this work.

Auduboni Group

The breeding range of this group is from central British Columbia, southern Alberta, and extreme southwestern Saskatchewan southward to northern Baja California, central Durango, and westernmost Texas, with a disjunct, resident population in extreme southeastern Chiapas and the adjacent highlands of Guatemala (Fig. 1). Except for the last, all populations are thought to be migratory, or at least are not known to be resident. Geographic variation exists in plumage color and pattern and in measurements.

Plumage variation.—In breeding plumage, males from north of the Mexican border are gray above streaked with black, and white below with the breast

streaked to solidly black. The loreal and anteriormost auricular areas are blackish, and the areas posterior to the auriculars and posterior to the yellow crown patch are gray or grayish white. Over much of the western United States, southwestern Canada, and Baja California this plumage varies only slightly, with males from the Southern Rockies and Black Hills southward averaging somewhat more extensively black on the underparts than those to the north and west. The increase in extent of black is gradual over most of this extensive area, but in the southernmost Southwest a marked increase occurs in the extent of black not only on the underparts but also on the sides of the head and in the dorsal streaking as well. This increase is most apparent in adult males of the Chiricahua and Huachuca Mountains of Arizona, but it also exists in first-year males from those areas and in males from northward to the Mogollon Plateau of Arizona and New Mexico (and occasionally farther). In the increased melanism specimens from the two Arizona mountain areas often are intermediate between more northern populations and those of the Sierra Madre Occidental. The latter are even more extensively black below, with heavier dorsal streaking, more blackish heads (lores, forehead, auriculars), and have the post-coronal and post-auricular patches whitish rather than grayish in color. Except for narrow intergradation through the Chiricahua and Huachuca Mountains, the Sierra Madrean population shows a discontinuity with both northern and southern populations in characters of the male breeding plumage.

Also distinctive is the resident population of Chiapas and Guatemala, in which males in breeding plumage are solidly black above, or black with a few gray streaks or smudges, with the post-coronal and post-auricular patches markedly white. The underparts are somewhat less extensively black than those of Sierra Madrean males.

In winter plumage adult males from north of the Mexican border have the upperparts extensively gray, washed with light to moderately dark-brown, and the black marking of the underparts (obscured by buff tips in fresh plumage) are in the form of spots or mottling. First-year males are browner, less gray above and have the ventral black markings as streaks. Females resemble first-year males but are more diffusely and less darkly streaked and in first-year plumage have reduced or no yellow in the throat. North of the southernmost Southwest little geographic variation exists in these plumages, although adult males become slightly more extensively black below as one progresses southward. In southern Arizona, and at least occasionally farther northward, occurs a definite shift toward the winter plumages that characterize the birds of the Sierra Madre Occidental, with the populations of the Chiricahua and Huachuca Mountains constituting intergrades in winter plumages between the Sierra Madrean populations and those to the north.

Adult males in winter plumage from the Sierra Madre Occidental are more extensively gray above with heavier black streaking than those from farther north, and the uneven brown wash that may be present is darker brown. The underparts are much more extensively black (with a variable buff wash in fresh plumage) and the face is blackish. First-year males and females are darker brown above, heavier streaked, and more extensively black below than their northern counterparts. Specimens of this population are highly separable from those farther north, except for a few of the intergrade specimens from southernmost Arizona.

Also distinct and highly separable in winter plumage is the population of the Chiapas-Guatemalan area. Adult males differ from all others in having the winter plumage identical to the breeding plumage, thus lacking any trace of buff or brown. First-year males and females resemble each other and their counterparts from the Sierra Madre Occidental, differing from the latter in their more richly brown, less sooty upperparts and more extensive streaking on the occiput.

Females in breeding plumage show a pattern of geographic variation that parallels that of the breeding plumage of males and winter plumages. The same pattern of geographical variation also exists in the juvenal plumage as far as is known, but in the absence of specimens from the Chiapas-Guatemalan area the situation there remains to be clarified. In each of these plumages no significant geographic variation exists in populations north of the Mexican border except in southernmost Arizona (occasionally elsewhere in the Southwest), where intergradation from northern plumage types toward that of the Sierra Madre Occidental occurs. For example, north of the intergrade area the upperparts of juveniles vary from light gray to buffy brown and the blackish streaking is narrow above and below. In the Sierra Madre Occidental the upperparts are a darker, more rufescent brown, lacking any grayish cast, and the streaking is darker, broader, and more extensive. Interestingly, the Sierra Madrean juveniles are virtually identical to those of the *coronata* group except for being more extensively streaked above and relatively larger in size. I presume that Chiapas-Guatemala juveniles will be found to be similar to those of the Sierra Madre Occidental.

Geographic variation was found to exist also in the amount of white in the outer rectrices. North of the Mexican border the average scores of white in the tail of 14 samples showing no introgression with *coronata* were 4.9 to 5.1 in adult males, compared to 4.6 in the Sierra Madre Occidental and 4.4 in the Chiapas-Guatemalan area. In first-year males showing no introgression from the north the values are 4.2 to 4.7, compared with 3.8 in both the Sierra Madre Occidental and Chiapas-Guatemalan area; females from the respective areas score 3.7 to 4.6, 4.3, and 3.8. These figures show

that males of the Mexican-Guatemalan area average less white in the tail than those from farther north, but in females considerable overlap exists. No effective separation of populations is possible on this basis because of the amount of individual variation.

Mensural variation.—In the *auduboni* group at least local geographic trends are evident in body weight and lengths of culmen, tarsus, and wing. Slightly lesser values of weight are evident in 4 of 5 western United States samples (range of means 11.9 to 12.2, ± 0.7 to 1.0 grams) compared to 5 Rocky Mountain and Southwest samples (range of means 12.5 to 13.0, ± 0.6 to 1.5 grams), but differences are not significant and one western sample (northwestern California— 12.6 ± 0.6 grams) overlaps the eastern range. The Sierra Madre sample (mean 12.7 ± 0.7 grams) and the one Guatemalan weight (13.0) are similar to more northern values and suggest a general homogeneity in this character in the *auduboni* group.

Much of the variation in culmen length in the *auduboni* group is mosaic rather than clinal in nature, although certain populations are distinguishable compared to others. For example, in the Chiapas-Guatemalan area culmen length averages significantly larger (value 7.9 ± 0.2 mm in females and first-year males, 8.1 ± 0.1 mm in adult males) than in the Sierra Madrean population (females 7.2 ± 0.3 mm, males 7.4 ± 0.2 mm). Among the northern populations values vary widely (7.1 to 7.9 in females, 7.1 to 8.1 mm in males), but the pattern of variation is mosaic and no effective separation is possible *inter se* or when compared with more southerly populations.

A gradual cline of increasing tarsus length exists from the north to the south, but as in culmen length local digressions and mosaic variation are present. For example, minimum values are in the Northwest Coast sample (17.7 to 18.0, ± 0.4 to 0.5 mm, depending on age and sex) compared to maximum values (18.9 to 19.4, ± 0.5 to 0.6 mm) which occur in the Chiapas-Guatemalan area. Because of intergradation, overlap, and variability, no segregation of populations is possible on this basis.

A generally orderly and gradual cline of increase of wing length occurs from the Northwest Coast southward to the Chiapas-Guatemalan area (Table 1). Differences in the means of these two extreme areas are 7.3 to 7.8 mm and are highly significant, but because of the gradual nature of intergradation, no line can be made that will separate adjacent populations on a reliable and large-scale basis. Even when populations from geographic extremes are compared one finds that separation is not highly effective. For example, the values in the Chiapas-Guatemalan sample average larger than all other *auduboni* samples, but no significant differences exist between that sample and those from the Sierra Madre Occidental, Southwest, Southern Rockies, and the Black Hills. North of the Mexican border the effective separation of

populations is equally untenable because of the very broad overlap, and the small average differences between extremes.

Interestingly, I found no differences between migratory and non-migratory populations in relative lengths of the "wingtip" (i.e., the ratio of the length of the primaries posterior to the tips of the secondaries on the folded wing to the length of the total wing.). For example, this ratio is 24.5 per cent in adult males of the resident Chiapas-Guatemalan population compared to 24.1 per cent in the highly migratory Black Hills population.

Summary of variation and nomenclatural conclusions.—This review of geographic variation reveals the existence of plumage characters which reliably and on a large scale distinguish several populations at the level of formal subspecies. These characters include the extent of black in male plumages, color of the upperparts and amount of streaking in breeding, winter, and juvenal plumages, and the color of the post-auricular and post-coronal patches in breeding males. These characters involve stepped or broken clines of increasing melanins in the plumage (decreasing in the post-auricular and post-coronal patches) from north to south. Clines of increasing tarsus and wing lengths occur over the same area but no steps or breaks exist that permit effective separation of adjacent (and many distant) populations. Also the weak clines or locally mosaic variations in the amount of white in the outer rectrices, body weight, and culmen length are generally ineffective in separating most populations although the last effectively separates breeding birds of the Chiapas-Guatemalan area from those of the Sierra Madre Occidental. Populations meriting formal, subspecific recognition are *goldmani* (Nelson, 1897), resident of the Guatemalan highlands and adjacent Chiapas (Fig. 1, sample 42); *nigrifrons* (Brewster, 1889), breeding in the Sierra Madre Occidental of Chihuahua and Durango (Fig. 1, sample 41); and *auduboni* (Townsend, 1837), breeding from Baja California and the Southwest northward (Fig. 1, samples 18 through 40), intergrading with the preceding in the Chiricahua and Huachuca Mountains of southern Arizona. The name *memorabilis* (Oberholser, 1921) applied to the breeding birds of the Southern Rockies, etc., is not recognizable because of broad intergradation in wing length and plumage characters with northwestern populations. However, infra-subspecific segregation of long- and short-winged extremes of the interior and the Northwest Coast populations, respectively, may be useful and is provided for in the key.

KEY

This key is intended both as a summary of taxonomically useful geographic variation and as a synopsis of populations, named and otherwise, which can be reliably segregated on such bases. Segregates which are worthy of formal

subspecific recognition are identified only by name, whereas infra-subspecific ones are identified by breeding range with names that have been applied to them in quotes. The intergrade populations which bridge *coronata* and *auduboni* and those which bridge *auduboni* ("memorabilis") and *nigrifrons* are not included. Characters given here yield identifications which have a 95 per cent or better probability of accuracy.

1. Light brown to white post-ocular line present in winter and breeding plumages; throat light brown to white in all plumages; white in outer 2 to 3 pairs of rectrices in most females and first-year males and in outer 3 to 4 in most adult males. ----- *coronata*
 - a. Minimum wing lengths: females—73.5 mm, first-year males—75.5 mm, adult males—78.0mm ----- breeding populations of Alaska, Yukon, MacKenzie Delta, northwestern British Columbia ("*hooveri*").
 - b. Maximum wing lengths: female—69.0 mm, first-year males—72.0 mm, adult males—74.0 mm; includes all males with solidly black breasts in breeding plumage ----- breeding populations from MacKenzie and northeastern British Columbia eastward to the Atlantic Coast.

1. Post-ocular line absent in winter and breeding plumage; throat yellow in breeding plumage and yellowish (at least in malar region) in winter plumage, except in some first-year females and (rarely) males which have none; white in the outer 4 pairs of rectrices in most females and first-year males and in outer 5 in most adult males (if not wing exceeds 74.5 mm in females, 78.5 mm in first-year males, 80.5 mm in adult males). ----- 2

2. Breeding-plumaged male gray above lightly streaked with black, breast streaked to solidly black and sides streaked with black; female grayish to light brown above, lightly streaked with blackish on upperparts, breast, and sides. Winter-plumaged adult male gray above streaked with black and variably washed with light brown or light rufous brown, breast spotted or mottled with black and washed with buff; first-year male similar but more extensively brown (less grayish) above and with blackish on breast as streaks; females similar to last but streaking paler and much more diffuse ----- *auduboni*
 - a. Maximum wing length: females—71.0 mm, first-year males—74.0 mm, adult males—77.0 mm ----- breeding populations of costal areas of British Columbia, Washington, and Oregon.
 - b. Minimum wing lengths: females—76.5 mm, first-year males—78.5 mm, adult males—81.0 mm ----- breeding populations of the Rockies, Black Hills, Great Basin, Sierra Nevada, and southwestern United States ("*memorabilis*").

2. Breeding-plumaged males more extensively black above and below; females darker above and with heavier streaking above and below. Winter-plumaged males more extensively gray or black above and more extensively black below; first-year males and females darker brown above and with heavier streaking above and below than *auduboni* ----- 3

3. Breeding-plumaged males gray above with heavy black streaking, sides and front of head washed with blackish, breast, sides, and posterior abdomen solidly black, post-auricular and post-coronal patches grayish white; female sooty to moderately

dark brown above with moderate streaking on the crown. Winter-plumaged adult male extensively gray above with considerable black streaking and variable (but usually limited) wash of dark rufescent brown, below mottled or solidly black on the breast, sides, and posterior abdomen, washed with buff; first-year male similar but less grayish, more extensively brown above and black of underparts usually as spotting; female similar to last but not as dark brown above with lighter streaking and with blackish of underparts as streaks *nigriifrons*

3. Breeding-plumaged males solidly black above or with limited gray streaking or mottling, breast and sides solidly black but posterior abdomen white, post-auricular and post-coronal patches white; female browner less sooty above with heavier streaking on the occiput. Winter-plumaged adult male identical to breeding male, lacking browns or buff in plumage; first-year male grayer, less brownish above with more extensive streaking than *nigriifrons*; female is richer, less sooty above with heavier streaking on the occiput than *nigriifrons* *goldmani*

SUMMARY

Geographic variation in plumage and measurements is discussed in the *Dendroica coronata* (L.) complex, consisting of two semispecies *coronata* and *auduboni* Townsend, particularly with reference to features which bear on segregation of populations, either as formal subspecies or as "infra-subspecies." The latter are populations that have some distinctive character(s) by which individuals can be identified, but which lack sufficient separability to warrant formal recognition. In the *coronata* group only the nominate race is formally recognized, although breeding populations of northwestern North America ("*hooveri*" McGregor) are infra-subspecifically separable from more easterly ones on the basis of extremes in wing length, i.e., long versus short. In the *auduboni* group three subspecies are recognized: *auduboni*, *nigriifrons* Brewster, and *goldmani* Nelson. Within the first, infra-subspecific segregation of breeding populations in the coastal northwest from those of the interior ("*memorabilis*" Oberholser), is possible on the basis of extremes of wing length, i.e., short versus long. Because of the largely clinal or mosaic nature of mensural variation, the characterization of the four accepted subspecies in this complex is basically on plumage characters. Plumage characters also show clinal gradation but discontinuities or steps in the clines are such that formal naming of subspecies is justifiable. The provision for the identification of infra-subspecies is to allow study of dispersal and other features in populations which have identifiable extremes but which are not sufficiently separable to warrant formal, subspecific recognition.

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NESTING BIRD ECOLOGY OF FOUR PLANT COMMUNITIES IN THE MISSOURI RIVER BREAKS, MONTANA

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THE Missouri River "Breaks" is a name that has been applied to that section of the immediate Missouri River Valley which stretches approximately 180 miles between Fort Benton and the Fort Peck Reservoir, Montana. This stretch of the river is divided by topographic features into three separate units—The Fort Benton-Virgelle unit, the White Rocks-Badlands unit, and the Fort Peck Game Range. This region is of particular interest since it represents a stretch of the river that retains much of the same aspect as when first seen by Lewis and Clark, fur trappers, and steamboat passengers.

Because of the tremendous size of the "breaks" area, my studies were concentrated in that area known as the White Rocks-Badlands unit which originates approximately 42 river miles downstream from Fort Benton in north-central Montana. This area was selected because of its limited accessibility, "pristine" wilderness aspect, because there have been no published avifaunal investigations for this specific area, and lastly, because the U.S. Army Corps of Engineers has proposed several dam sites for water-resource development. Inundation would destroy the most unique geological, historical, paleontological, and biological features found in this stretch of the river. The study area consisted of a straight-line distance of about 33 miles (45 river miles). The purpose of this paper is to describe the breeding bird populations of the major habitats and to establish certain ecological relationships between these populations and their communities. Preliminary observations were made in 1967 with quantitative data obtained during the summer of 1968.

METHODS

Study areas were selected in each vegetation type that were typical of that type and that had a minimum amount of disturbance. Study areas in the greasewood-sagebrush shrubland, sagebrush grassland, and pine-juniper woodland were 40 acres in size with dimensions of 660 × 2640 feet. Each area was censused at 220 foot intervals. Because of the strip-like nature of these areas, one source of error present in mapping territories is that some territories included some area beyond the boundaries of the study zone. Care was taken, where possible, to select areas with physiographic barriers and distinct plant communities isolating such areas, thereby reducing the error. Located on an abandoned meander, the study area in the cottonwood forest consisted of an area 17.5 acres in size and was censused at 150 foot intervals.

Breeding bird populations were studied with the aid of composite census maps similar to those described by Kendeigh (1944). Descriptive data on such maps included birds seen and singing males, location of active nests, eggs per nest, young out

of the nest, and behavioral activities related to nesting. Long poles, to tap silver sagebrush (*Artemisia cana*) plants, aided in flushing nesting birds during each census in the sagebrush-grassland community. A Labrador dog was also used in this type for flushing Ring-necked Pheasants.¹

Census periods and times for each study plot were as follows: cottonwood forest (8 trips, 2-8 June; census time, 06:00-09:30), sagebrush-grassland (6 trips, 9-14 June; 06:00-08:30), greasewood-sagebrush shrubland (6 trips, 16-21 June; 06:00-09:00), pine-juniper woodland (6 trips, 25-30 June; 06:00-10:00). Visits to the plots for other purposes supplied confirmatory data beyond the time spent in formal censusing.

The method of vegetation analysis was a modification of this method of Daubenmire (1959), whereby 2 × 5 dm plots were systematically placed within a relatively homogenous and undisturbed portion of each habitat studied. Measurements were also taken at nest sites for certain avian species to attempt to ascertain nesting requirements, whereby 20 × 50 foot sample units, each containing 20 systematically arranged 2 × 5 dm plots enclosed separate nest sites. The per cent canopy coverage of each taxon (per cent of area covered by foliage), the average frequency (percentage occurrence among plots), and percentage of bare ground, rock and lichens were recorded for each plot. Canopy coverage classes were: 1 = 0-5 per cent; class 2 = 5-25 per cent; class 3 = 25-50 per cent; class 4 = 50-75 per cent; class 5 = 75-95 per cent; and class 6 = 95-100 per cent. The midpoint of each class was the value used in data tabulations. Comparative data for these types are presented in Table 1. The botanical nomenclature follows that of Booth (1950) and Booth and Wright (1959).

VEGETATION

The study area lies in the Prairie Biome, more specifically, the Mixed Prairie which is composed predominantly of mid and short grasses. Vegetation in the White Rocks-Badlands unit is varied due to ridges, sharply cut coulees, and creek bottoms. The major plant communities in the study area are as follows:

Greasewood-Sagebrush Shrubland.—Where clay soils containing considerable amounts of sodium occur, the vegetation is characteristically sparse and dominated by greasewood (*Sarcobatus vermiculatus*)—a point established by Mackie (1965). Distribution of greasewood, big sagebrush (*Artemisia tridentata*), and silver sagebrush ranges from sparse to moderate along Missouri River bottomlands, coulee-bottom benches, small alluvial fans, and hills with exposed bentonite beds. Principal forbs include woolly plantain (*Plantago purshii*), western stick tight (*Lappula redowskii*), littlepod false flax (*Camelina microcarpa*), and plains prickly pear (*Opuntia polycantha*). Dominant grasses include downy chess brome (*Bromus tectorum*), western wheatgrass (*Agropyron smithii*), and desert saltgrass (*Distichlis stricta*).

Sagebrush Grassland.—Relatively dense stands of silver sagebrush ranging in height from two to six feet occur extensively along the Missouri River bottom lands and coulee bottoms having intermittent stream flow. Western wheatgrass, the former dominant in this type, has been greatly replaced by the invader downy chess brome. The distribution and fluctuation of these two grasses is related to livestock distribution and intensity of grazing. In areas where extensive grazing has occurred in silver sagebrush, subsequent erosion has produced hard, clay-pan soils, with reduced vegetative cover. Meadow barley (*Hordeum brachyantherum*), woolly plantain, and littlepod false flax are common in such areas. The canopy coverage for silver sagebrush is more extensive and the total forb and grass coverage is greater than that of the greasewood-sagebrush shrubland.

¹ Scientific names of birds are given in Table 2.

TABLE 1 (Continued)

	Greasewood- Sagebrush Shrubland		Sagebrush Grassland		Pine- Juniper Woodland		Cottonwood Forest	
Trees								
<i>Pinus flexilis</i>								
<i>Juniperus scopulorum</i>								
<i>Juniperus communis</i>								
<i>Populus sargentii</i>								
<i>Fraxinus pennsylvanica</i>								
<i>Acer negundo</i>								
Rocks	1	18			5	41		
Lichens	5	72	1	13	1	25		
Bare Ground	20	88	3	25	28	79		

Pine-Juniper Woodland.—This community occurs extensively on slight to moderately steep slopes in those areas where Eagle Sandstone is exposed. Stands of limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*) are typically scattered in these areas. The understory shrub layer is composed of common juniper (*Juniperus communis*) and skunkbush sumac (*Rhus trilobata*). Principle forbs and grasses include hood's phlox (*Phlox hoodii*), *Carex* spp., and junegrass (*Koeleria cristata*). Small hills with moderately cut drainageways separating such stands are common. Such areas support a variable vegetation comprised of dense growths of skunkbush and common juniper in the drainageways, and big sagebrush, plains prickly pear, yucca (*Yucca glauca*) and needle and thread (*Stipa comata*) on the periphery.

Cottonwood Forest.—The cottonwood habitat, dominated by plains cottonwood (*Populus sargentii*), is found along Missouri River bottom lands and on numerous islands in this reach of the river. The larger groves show three distinct strata. Cottonwood comprises the upper stratum (18–19 m); the second stratum consists of green ash (*Fraxinus pennsylvanica*) (2–11 m), and scattered box elder (*Acer negundo*); the third stratum consists of moderate to heavy thickets of western snowberry (*Symphoricarpos occidentalis*) and nootka rose (*Rosa nutkana*). Litter accumulation is quite heavy in the larger cottonwood groves resulting in limited growth of forbs and grasses. The most common forb is American vetch (*Vicia americana*) and the most common grass is blue-bunch wheatgrass (*Agropyron spicatum*). Heavy silting from flooding has undoubtedly influenced the species composition and vegetation grouping patterns in those areas subjected to a high frequency of flooding.

Other vegetation types of lesser importance found in the study area but not quantitatively analyzed include small islands covered with *Salix* spp. and low herbaceous growth; numerous long, open canyons with dissected drainageways that support a variable growth in vegetation; and limited stands of Douglas fir (*Pseudotsuga menziesii*) associated with limber pine.

RESULTS

Greasewood-Sagebrush Shrubland.—Lark Sparrows and Western Meadowlarks were the two most abundant species found in this habitat (Table 2).

TABLE 2
NESTING BIRDS (PAIRS PER 100 ACRES) FOUND IN FOUR PLANT COMMUNITIES OF THE
WHITE ROCKS-BADLANDS UNIT

Type of habitat	Greasewood- Sagebrush Shrubland	Sagebrush Grassland	Pine- Juniper Woodland	Cottonwood Forest
No. of acres	40	40	40	17.5
Species				
Ferruginous Hawk (<i>Buteo regalis</i>)				6
Pigeon Hawk (<i>Falco columbarius</i>)				6
Sparrow Hawk (<i>Falco sparverius</i>)				6
Ring-necked Pheasant (<i>Phasianus colchicus</i>)		5		
Mourning Dove (<i>Zenaidura macroura</i>)	b	5	50	13
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)				a
Great Horned Owl (<i>Bubo virginianus</i>)				6
Saw-whet Owl (<i>Aegolius acadicus</i>)			3	
Common Nighthawk (<i>Chordeiles minor</i>)			a	
Red-shafted Flicker (<i>Colaptes cafer</i>)				6
Downy Woodpecker (<i>Dendrocopos pubescens</i>)				13
Eastern Kingbird (<i>Tyrannus tyrannus</i>)				13
Western Kingbird (<i>Tyrannus verticalis</i>)			3	13
Least Flycatcher (<i>Empidonax minimus</i>)				13
Western Wood Pewee (<i>Contopus sordidulus</i>)				a
Cliff Swallow (<i>Petrochelidon pyrrhonota</i>)			a	
Black-billed Magpie (<i>Pica pica</i>)				6
Black-capped Chickadee (<i>Parus atricapillus</i>)				13

TABLE 2 (Continued)

Type of habitat	Greasewood- Sagebrush Shrubland	Sagebrush Grassland	Pine- Juniper Woodland	Cottonwood Forest
No. of acres	40	40	40	17.5
House Wren (<i>Troglodytes aedon</i>)			5	45
Rock Wren (<i>Salpinctes obsoletus</i>)			5	
Catbird (<i>Dumetella carolinensis</i>)				13
Brown Thrasher (<i>Toxostoma rufum</i>)			8	
Robin (<i>Turdus migratorius</i>)			15	26
Swainson's Thrush (<i>Hylocichla ustulata</i>)				13
Veery (<i>Hylocichla fuscescens</i>)				a
Cedar Waxwing (<i>Bombycilla cedrorum</i>)				13
Loggerhead Shrike (<i>Lanius ludovicianus</i>)			5	
Starling (<i>Sturnus vulgaris</i>)				19
Red-eyed Vireo (<i>Vireo olivaceus</i>)				19
Yellow Warbler (<i>Dendroica petechia</i>)				52
Yellowthroat (<i>Geothlypis trichas</i>)				13
American Redstart (<i>Setophaga ruticilla</i>)				19
Western Meadowlark (<i>Sturnella neglecta</i>)	25	10	13	
Baltimore Oriole (<i>Icterus galbula</i>)				6
Bullock's Oriole (<i>Icterus bullockii</i>)				13
American Goldfinch (<i>Spinus tristis</i>)				6
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)			8	13

TABLE 2 (Continued)

Type of habitat	Greasewood-Sagebrush Shrubland	Sagebrush Grassland	Pine-Juniper Woodland	Cottonwood Forest
No. of acres	40	40	40	17.5
Lark Bunting (<i>Calamospiza melanocorys</i>)	5			
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)				6
Vesper Sparrow (<i>Pooecetes gramineus</i>)		5		
Lark Sparrow (<i>Chondestes grammacus</i>)	30	5	18	
Chipping Sparrow (<i>Spizella passerina</i>)			13	
Brewer's Sparrow (<i>Spizella breweri</i>)	5	48		
Total pairs per 100 acres	65	78	146	390

^a Indicates species present on study area but density low or difficult to assess.

^b Indicates species which nested outside the study plot in this habitat and species frequently observed but not definitely known to nest in the study plot.

These species comprised 46 per cent, and 39 per cent, respectively, of the total breeding population.

Although the presence of greasewood and big sagebrush appears to be a nesting requirement for the Lark Sparrow, nest data indicate more specific nesting requirements with regard to big sagebrush. Of the eight Lark Sparrow nests located, seven were found on the ground directly under big sagebrush, but only one under greasewood. Vegetative measurements taken at four separate nests, based on four 20 × 50 sample units showed greasewood with a canopy coverage averaging 14 per cent and life form measurements of 0.37 m (height of shrub) × 0.6 m (width of crown). Big sagebrush had similar life form measurements of 0.54 × 0.62 m and a canopy coverage averaging 15.6 per cent. Examination of Table 1 shows that the average frequency ratings for both shrubs were quite similar.

A comparison of the life forms for big sagebrush and greasewood shows that the former has many more overhanging branches that could be used for nest concealment and protection. The lowermost branches of greasewood, in contrast, are more upright thereby providing less overhang and coverage. Because the lowermost branches of greasewood are not positioned as well as those of big sagebrush to intercept rainfall, the soil tends to be more compact forming a "hardpan" layer under the plants. The surface soil texture

under big sagebrush is more granular, has a higher percentage of litter, and lacks this hardpan consistency. It seems quite probable that nest depressions could be excavated with greater ease in such a substrate. The difference in soil porosity for these two shrubs strongly suggests that porosity may be an important factor in nest selection.

The Western Meadowlark was found in areas having more herbaceous and grass cover and with more widely dispersed shrubs than were present in the habitat of the Lark Sparrow. Each of the two meadowlark nests located was built adjacent to the paddles of prickly pear cactus. Two meadowlark nests found in the pine-juniper woodland were similarly located in prickly pear cactus. Cameron (1907) also reported a nesting bird in a cactus patch for eastern Montana.

Sagebrush-Grassland.—The most abundant species, Brewer's Sparrow, comprised 61 per cent of the total breeding population for this habitat.

After charting the locations of 15 active Brewer's Sparrow nests on the composite census maps, it was evident that this species preferred silver sagebrush areas having a canopy coverage of around 50 per cent for nest sites. Quantitative measurements, based on 80 Daubenmire plots, showed substantial differences in the utilization of sagebrush by this species for nesting purposes. Most of the nests, eleven or 73 per cent, were found in silver sagebrush areas having a canopy coverage averaging 53 per cent. Shrubs averaged one meter high by 1.2 meters wide. Low density sagebrush areas in which one nest was found included shrubs having a canopy coverage of 24 per cent and physical measurements of 0.4×0.56 m. Three nests (20 per cent) were found in dense sagebrush areas averaging 1.4×1.6 m and had a canopy coverage of 81 per cent. The physiognomy or structure of the vegetation in this habitat appears to be quite important in the selection of nest sites thereby influencing the distribution of birds.

Feist (1968) in his study of five 40-acre plots of big sagebrush-grassland in central Montana, maintained that the Brewer's Sparrow preferred dense sagebrush areas for nest sites with a canopy coverage averaging 31 per cent. While there is some overlap in regard to the height and canopy coverage of silver sagebrush utilized by this species, it is my belief that dense silver sagebrush areas are used less frequently in comparison with those of big sagebrush.

Pine-Juniper Woodland.—Scattered stands of limber pine and juniper separated by open herbaceous-grassy areas with associated dissected drainageways containing numerous brush pockets, provided a diversified ecological community for nesting birds.

Mourning Doves, the most abundant nesting bird for this type, were dispersed throughout the study area and nests were located in all cover types.

TABLE 3

COMPARISON OF PER CENT CANOPY COVERAGE AND GROUND COVER CHARACTERISTICS AT LARK SPARROW NESTING SITES IN THE GREASEWOOD-SAGEBRUSH SHRUBLAND AND PINE-JUNIPER WOODLAND COMMUNITIES

Canopy coverage and ground cover characteristics	Greasewood-Sagebrush Shrubland	Pine-Juniper Woodland
Shrubs	15	18
Forbs and Grasses	45	44
Lichens	7	2
Rock	1	4
Bare ground	31	36

The ecological adaptability of the Mourning Dove in its ability to nest in conifers, deciduous trees, and a wide variety of shrubs as well as on the ground is well known (Bent, 1932). The dove selected a wide variety of nest sites on the study area. Of the 17 nests located, eight were located on horizontal branches of conifers with limber pine being the preferred species. Although Rocky Mountain juniper was common in the understory of limber pine, it showed a low frequency for nest sites. It was my impression that juniper was not selected for nest sites because of the typical dense and upright branches which result in a poor structural platform. The lowermost branches of limber pine, in contrast, are more horizontal and open, thereby providing more suitable nesting platforms. A horizontal branch appears to be the essential requisite for the nest platform in conifers. Hanson and Kossack (1963) found in their Illinois study of doves that blue spruce (*Picea pungens*) was preferred over four other conifers, including pine, because of its stiff, horizontal branches and needles which provided secure nesting platforms. Hardy (1945) found that the Mourning Dove in a Piñon-Juniper vegetation type preferred juniper to piñon pine (*Pinus edulis*) because the former has larger and more horizontal branches.

Other species showing a nesting preference for conifers were the Chipping Sparrow, Robin, and Loggerhead Shrike. Four of the five Robin nests located were in limber pine and they averaged 3.9 m off the ground. Although only one Chipping Sparrow nest was found, numerous old nests located, all in juniper, suggested that this was the preferred nesting site.

The third most abundant species, the Lark Sparrow, preferred big sagebrush areas similar to those in the greasewood-sagebrush habitat. Vegetative measurements taken at one nest site, based on 20 Daubenmire plots, showed an average total canopy coverage of 64 per cent. Comparison of these data with that of the greasewood-sagebrush habitat shows a remarkable similarity in nesting niches (Table 3).

Brushy, dissected drainageways, containing dense pockets of skunkbush sumac and common juniper provided nesting sites for the Brown Thrasher and Rufous-sided Towhee. Although such areas were not abundant, they were of importance to such species.

Cottonwood Forest.—This community supported the largest number and the greatest variety of species. Thirty species of birds utilized this type for nesting. The cottonwood community offers more opportunities for ecological specialization than the habitats found in the other communities examined. Since this community shows three well-defined strata, and since there were substantial differences in the utilization of each stratum for nesting, the birds for each will be described.

While there was some overlap in nesting niches among the various strata, 12 of the total breeding species nested in the upper cottonwood stratum (House Wren, Red-shafted Flicker, Bullock's Oriole, Downy Woodpecker, Western Kingbird, Baltimore Oriole, Sparrow Hawk, Black-billed Magpie, Great Horned Owl, Ferruginous Hawk, Pigeon Hawk, and Starling). About one-third of these were hole nesters. High intensity winds frequently occur in the "Breaks" area producing a large number of cottonwood culls which make such trees suitable for excavation.

The middle stratum (green ash with scattered box elder) had the lowest number of nesting birds. Eight species, of which the Robin was the most common, nested in this stratum. This stratum has fewer nesting niches in comparison with the upper stratum. For example, the number of culls for excavation were certainly fewer, thereby limiting hole-nesting species.

The lower stratum (rose and snowberry) provided nesting sites for ten species. Vegetation measurements for this stratum showed a total average canopy coverage of 74 per cent. Shrubs (rose and snowberry) averaged 62 per cent with forbs and grasses averaging four per cent. Although snowberry had an average frequency rating similar to that of rose, no nests were found in this shrub. A comparison of life forms shows snowberry as a shrub with numerous slender, drooping branches; rose in contrast, is a more erect shrub having stouter branches armed with numerous spines thereby providing more suitable nesting crotches. This stratum provided the least variety of nesting niches. Typical nesting birds utilizing this stratum were the Yellow Warbler, American Goldfinch, Swainson's Thrush, Catbird, and Veery.

Forest edge species (Rufous-sided Towhee, Yellowthroat, Grasshopper Sparrow, Eastern Kingbird) utilizing rose thickets bordering and encroaching into the sagebrush-grassland community seldom penetrated the cottonwood interior for more than 10–20 feet.

DISCUSSION

The general pattern of the utilization by birds of each habitat for nesting reflects the basic physiognomy or structure of the vegetation. Although there is a certain amount of overlap in plant species and configuration used for nesting, data from this study show that some bird species show a very close adherence to a specific life form of vegetation present, while others are more flexible in using the overall habitat. The Lark Sparrow, for example, appears partial to nesting under big sagebrush while the Mourning Dove is quite adaptable in being able to use a variety of vegetation for nest sites.

The greasewood-sagebrush community is the poorest in species composition and relative density. The density for the five breeding species averaged 65 pairs per 100 acres. The implication is that a low density and productivity of vegetation allow for a low diversity and density of breeding birds. That this suggestion is not necessarily correct is suggested by the data presented earlier in which although big sagebrush and greasewood have similar life forms and frequency ratings, the more granular type soil found under big sagebrush appears to be an important factor in determining Lark Sparrow densities.

The sagebrush-grassland community supported six species with a total nesting density of 78 nesting pairs per 100 acres. As pointed out above, the general pattern of distribution of Brewer's Sparrows in this habitat was a concentration in those areas with shrubs having a canopy coverage averaging 50 per cent. It is possible that shrubs found in such areas may provide more suitable nest sites with overhanging branches that serve to conceal and protect the nest; or perhaps the foliage volume for such shrubs plays an important factor in limiting densities. It is also possible that a difference in the nesting density of Brewer's Sparrow is not under sole control of differences in shrub density and canopy coverage.

The pine-juniper woodland provided a diversified ecological community for nesting birds supporting 14 species and 146 pairs of nesting birds per 100 acres. The high density of Mourning Doves in this habitat is partly explained by the versatility of the species in being able to use a heterogeneous mixture of plant life forms for nesting. Examination of Table 2 shows that the dove was the only species having the ecological adaptability to nest in all of the habitats studied, therefore having the greatest density of breeding birds for the entire study area.

The multi-storied vegetation structure of the cottonwood forest supports the greatest total biomass and contains the largest population of nesting birds (390 pairs per 100 acres) and the greatest number of species (30). Thus, as a natural habitat, the cottonwood forest can be shown to offer more opportunities for ecological specialization than the other habitats.

The information summarized in Table 2 is of value in the sense that it presents an instantaneous description of the four avian communities, but it is incomplete. The reasons for this are: (1) Breeding bird measurements were taken during only a part of the breeding season so the true population might vary from the density figures given. (2) It is not realistic to suggest that the density of nesting pairs of birds per 100 acres for the hawks, owls, kingbirds, and doves in the cottonwood forest is correct. This habitat served primarily to supply nesting sites for these species, and because of the variability of neighboring habitats, it is difficult to make meaningful population adjustments for them. (3) As Brewer (1967) points out, bird populations for a given habitat are a product of many factors, including geographical location of the plant community, geographical ranges of species able to use the habitat, and structural features of the vegetation. Another prime consideration is that of habitat change. There is an apparent difference in relative densities in the study area when comparing bird populations of the same community from one locality to another because of livestock disturbances. I have no quantitative data concerning the interrelationships that exist between livestock and vegetation in the White Rocks-Badlands unit. My observations indicate noticeable differences.

SUMMARY

Intensive studies of the nesting birds in four plant communities representative of the White Rocks-Badlands unit of the Missouri River "Breaks," Montana were conducted during the summer of 1967 and 1968.

The greasewood-sagebrush shrubland has the fewest species and lowest relative density of the four communities. Density for all breeding species averaged 65 pairs per 100 acres. The Lark Sparrow and the Western Meadowlark were numerically the most important species. Although life form measurements and frequency ratings for big sagebrush and greasewood are similar in this habitat, a more granular soil under big sagebrush appears to be a nesting requirement for the Lark Sparrow.

The sagebrush-grassland community supported six species and 78 pairs per 100 acres. The Brewer's Sparrow was by far the most abundant species. The greatest density of nesting Brewer's Sparrows was found in silver sagebrush areas having a canopy coverage of around 50 per cent.

The pine-juniper woodland provided a diversified ecological community for nesting birds and supported about 146 pairs per 100 acres. The Mourning Dove was numerically the most important and was the only species having the ecological adaptability to nest in all of the major habitats found in the study area.

The cottonwood community supported the largest population of nesting birds (390 pairs per 100 acres) and the greatest number of species (30). This community provided more opportunities for ecological specialization and nesting sites than the habitats in the other communities because of its multi-storied vegetation and greater total biomass.

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29 AUGUST 1969. (ORIGINALLY RECEIVED 27 FEBRUARY 1969.)

NOTICE

Members who know students that are interested in ornithology now should send nominations to the Student Membership Committee addressed to Douglas James, Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701. The nominees will be invited by the committee to apply for membership in the Wilson Ornithological Society.

OLDSQUAWS NESTING IN ASSOCIATION WITH ARCTIC TERNS AT CHURCHILL, MANITOBA

ROGER M. EVANS

THE tendency for the Oldsquaw (*Clangula hyemalis*) to nest in close association with the Arctic Tern (*Sterna paradisaea*) has been noted in several geographic regions, including Alaska (Bailey, 1925, 1943), Southampton Island (Sutton, 1932), Greenland (Salomonsen, *in* Larson, 1960), and Spitsbergen (Lovenskiold, 1954; Burton and Thurston, 1959). Taverner and Sutton (1934) reported both species as common breeders along the west coast of Hudson Bay, near Churchill, Manitoba, but did not refer explicitly to association of nests of the two species. That such associations do occur in this region, however, is indicated by the observations of Twomey (*in* Taverner and Sutton, 1934) that populations of both species nested on a single small offshore island. Hawksley (1957:66) states that "the Old-squaw is commonly found nesting with Arctic Terns in North America," and implies that such associations occur at Churchill, but does not indicate the locations or extent of the association in this region. Evidence that close associations between nests of Oldsquaw and Arctic Tern are common on the mainland at Churchill, and particularly on small islands in fresh-water ponds, is presented below.

Larson (1960) has suggested that nest associations such as those mentioned above are commensal, the Oldsquaw deriving a degree of protection from potential nest predators as a result of the well-developed nest defense behavior of the Arctic Tern. The interpretation that protection from nest predators is derived by the Oldsquaw or other species, notably the eider (*Somateria*) and brant (*Branta bernicla*; *B. nigricans*) when they nest in association with Arctic Terns, has also been advanced by several other investigators, including Lovenskiold (1954), Gudmundsson (1956), Burton and Thurston (1959), Hilden (1965), and Cooch (1967). Koskimies (1957) and Vermeer (1968) have advanced the further hypothesis that imprinting of ducklings to gulls or terns nesting in the same vicinity may constitute the proximate cause of these and other similar associations.

The hypothesis that nest associations between Arctic Terns and Oldsquaws are commensal relationships that develop locally as a result of imprinting does not appear to have been subject to rigorous experimental tests. In the absence of such data, extensive documentation of the occurrence or non-occurrence of such nest associations in various local areas, including those where avian nest predators are common as well as those where such predators are rare or absent, would appear to be useful. The following ob-

TABLE 1
DISTANCE BETWEEN OLDSQUAW NESTS AND NEAREST OPEN WATER

Nest location	Number of nests	Distance to water (meters)		
		Mean	Median	Range
Mainland beach	3	9.0	9	8-10
Mainland tundra	9	28.6	1	0.2-200
Islands in fresh water	16	2.1	2	0.1-6.7

servations of the nest sites selected by Oldsquaws, the extent of their association with Arctic Terns, and the relationships of these associations to the more common avian predators in the Churchill region are presented here as a contribution towards such documentation.

DESCRIPTION OF NEST SITES

According to Phillips (1925), "there is nothing characteristic about the (Oldsquaw) nest or its site. It is usually near the water, though sometimes far away from it . . . and is placed under thick bushes . . . when such cover is found." Oldsquaws may nest as isolated pairs, or "practically in colonies" (op. cit., p. 362). This description applies with validity to the Oldsquaw nests observed at Churchill, where nests were found in virtually all major terrestrial areas, including (1) mainland beach, (2) mainland tundra, (3) islands in fresh-water ponds, and (4) offshore islands. The present observations, conducted during June and July of 1967 and 1968, were concerned primarily with the first three of these nest habitats; confirmation of the observations cited in Taverner and Sutton (1934) of Oldsquaws nesting on offshore islands was provided by Mr. Carroll Littlefield (pers. comm.), who counted seven Oldsquaw nests on a small island off the coast of Cape Churchill on 27 June 1968.

Although the Oldsquaw is said typically to nest along the edges of small fresh-water ponds or on islands in such ponds (Phillips, 1925; Bent, 1925), records of nests placed some distance away from the nearest open water are not uncommon. Bent (1925), for example, cited observations by Hersey of a nest placed 20 feet from the edge of a pond, and a report by Palmer of a nest 40 feet from a fresh-water pond. He further cited Ekblaw that nests are "sometimes in the grass near the pools, but more frequently . . . at considerable distances from any water" (Bent, 1925:38). At Churchill, the distances to the nearest open water were also variable, ranging from as little as 0.1 m to at least 200 m for the 28 nests measured (Table 1).

The distance between Oldsquaw nests and the nearest open water at Churchill was found to vary according to the area in which the nests were

TABLE 2
DISTANCE BETWEEN OLDSQUAW NESTS AND NEAREST ARCTIC TERN NEST

Nest location	Number of nests	Distance to nearest tern nest (meters)		
		Mean	Median	Range
Mainland beach	3	13	12	10-17
Mainland tundra	5*	72	70	18-178
Islands in fresh water	16	2.3	2	0.8-6

* Does not include three nests located in the vicinity of Arctic Terns but for which distances to tern nests were not determined, and one nest that was not in association with terns.

located (Table 1). Average distances were least on the small islands in fresh-water ponds (average for 16 nests, 2.1 m), somewhat greater along the beach (average for three nests, 9.0 m), and greatest in the mainland tundra (average for nine nests, 28.6 m). The average distance to water for the mainland tundra is skewed due to a number of extreme values well above the median distance of 1 m. Except for these extreme values on the mainland tundra, nest sites tended to be close to the shore for both fresh-water islands (median 2 m) and mainland tundra (median 1 m), and somewhat farther from water for nests located along the beach (median 9 m). These results suggest that Oldsquaws at Churchill exhibit a definite tendency to nest near the edge of water, but not exclusively so. This tendency is necessarily reinforced when small islands no more than a few meters in diameter are selected for nest sites, but may be relaxed when mainland tundra locations are selected. For nests located along the beach the minimum distance to water appeared to be set by the maximum extent of wave action at high tide.

In each of the three areas described above, Oldsquaws were found nesting in association with Arctic Terns. A similar association was also present on the small offshore island visited by Littlefield (pers. comm.). On islands in fresh-water ponds, Oldsquaw nests were found exclusively on islands that also contained Arctic Terns. In consequence, minimum distances between nests of the two species on these islands were necessarily small (average for 16 nests, 2.3 m), with none exceeding 6 m (Table 2). In the other areas, and particularly on mainland tundra, distances between Oldsquaw and Arctic Tern nests were greater, ranging up to at least 178 m (Table 2). In addition, one Oldsquaw nest was found on mainland tundra in an area that apparently lacked a local population of breeding terns. This latter finding, coupled with the greater distances between nests of the Oldsquaw and Arctic Tern on the mainland tundra (Table 2), suggests a relaxation in the tendency for association between the two species on mainland tundra compared to islands in fresh-water ponds.

It should be noted that nest hunting for Oldsquaws was concentrated in areas that contained Arctic Terns, and random sampling of large areas of habitat was not done. The high frequency of association between Arctic Terns and Oldsquaws found at Churchill may therefore be biased upwards, due to an undetermined number of Oldsquaw nests being located well away from areas containing terns. Several considerations suggest, however, that the possibility of such a bias does not negate the conclusion that an association between the species does in fact occur, especially for those nests located on islands in fresh-water ponds. As indicated above, all 16 Oldsquaw nests found on such islands were in close association with Arctic Terns. While searching for nests in these areas, many islands in addition to those found to contain tern nests were inspected, yet in no instance was an Oldsquaw nest found on an island that lacked terns. Nests located on islands in one small fresh-water pond are illustrative: In 1967, two islands in the pond each had one Oldsquaw nest and one tern nest. In 1968, one of these islands had an Arctic Tern nest and two Oldsquaw nests; the other island contained nests of neither species. From considerations such as these, coupled with the measurements listed in Table 2, it seems reasonable to conclude that a definite positive association between Oldsquaw and Arctic Tern nests was present at Churchill in 1967 and 1968. An exact determination of the frequency of this association on mainland tundra remains lacking, however, pending a more complete and random sampling of the potential nesting habitat.

AVIAN PREDATORS

At least three potential avian predators of Oldsquaw eggs were present at Churchill: Herring Gull (*Larus argentatus*), Parasitic Jaeger (*Stercorarius parasiticus*), and Common Raven (*Corvus corax*). Of these species, the Herring Gull was most common; 15 and 22 breeding pairs were found, widely scattered, throughout the study area in 1967 and 1968 respectively. In addition, mixed flocks composed largely of non-breeders of this and other large *Larus* gulls totalling several hundred in number could be observed daily at the local garbage dump located near the middle of the study area.

Egg predation of ground-nesting species by Herring Gulls is considered by some authorities to be infrequent (Bent, 1921:112). They are, however, known to take eggs of various ground-nesting species (Tinbergen, 1953), including those of the Oldsquaw (Sutton, 1932:263-264). This latter fact, coupled with the high numbers of Herring Gulls known to be present at Churchill, suggests that it would be unrealistic to exclude the Herring Gull as a potential egg predator of Oldsquaws in this region.

Although less abundant than the Herring Gull, Parasitic Jaegers and Ravens were observed throughout the area in both 1967 and 1968. Accord-

ing to Kortwright (1953:283), jaegers, along with various other predators, may "take a heavy toll" of Oldsquaw eggs. Sutton (1932) also cited the Parasitic Jaeger as a predator of Oldsquaw eggs, and cited observations of jaegers taking Oldsquaw young. The Raven, according to Larson (1960), may also constitute an important egg predator of the Oldsquaw.

Despite the presence of the above predators, loss of Oldsquaw clutches at Churchill was limited. On islands in fresh-water ponds, no predator-destroyed clutches were found in 1967, even when nests were visited repeatedly, every one to two days, by one or more observers. In 1968, two clutches, found prior to the onset of nesting by the terns, were missing on subsequent visits to the islands, and may therefore have been destroyed by predators. On the beach, one nest was destroyed within an abandoned tern colony. This loss, however, was apparently due to wave action rather than to predation. On the mainland tundra, at least two, and possibly three, nests were destroyed, presumably by predators. Taken together, these figures indicate that at most, no more than five of the 28 nests (18 per cent) were destroyed by predators. This percentage loss of clutches compares favorably with egg loss (average 22.9 per cent) of several anatid species nesting in larid colonies located on islands in the Gulf of Bothnia (Hilden, 1964), but is somewhat greater than that for Gadwall (*Anas strepera*) and Lesser Scaup (*Aythya affinis*) nesting in association with *Larus* spp. in Alberta, where 89-90 per cent of the nests hatched (Vermeer, 1968).

DISCUSSION

In the absence of comparative data from areas where egg predators are absent or where terns and Oldsquaws do not nest together, definite conclusions concerning the extent of nest protection derived by the Oldsquaws that nest in association with Arctic Terns are not warranted. Indirect evidence, however, is provided by instances in which avian predators have been attacked and driven away by Arctic Terns, as described for the Herring Gull by Sutton (1932), Bullough (1942), and Sutton and Parmelee (1956). Active defense by Arctic Terns of their nest sites against Parasitic Jaegers (Anderson, 1913; Sutton, 1932; Lovenskiold, 1954) and Ravens (Sutton, 1932; Larson, 1960) have also been documented. Instances in which Arctic Terns attacked and chased these species were also observed during the present study at Churchill. There thus seems little reason to doubt the interpretation of Anderson (1913), Larson (1960) and others that such attacks by Arctic Terns provide a measure of protection for birds that nest in or near their colonies, and that such nest associations are therefore commensal relationships. The data obtained at Churchill suggest, however, that the commensal relationship between Oldsquaws and Arctic Terns is of significance primarily for nests located on islands (cf. also Larson, 1960;

Delacour, 1959:174–175), and possibly for those located on the beach, but is probably of less importance for nests located on the mainland tundra.

The most parsimonious explanation of the proximate mechanisms underlying the association between Oldsquaws and Arctic Terns is that of similar habitat preferences by two compatible species. At Churchill, this simple interpretation would seem sufficient for nests located on the mainland tundra, where distances between nests of the two species were comparatively great, but it does not appear sufficient to account for the close association in other habitats, particularly on islands in fresh-water ponds. In these latter areas, some form of active selection of one species by the other seems likely.

According to the general hypothesis advanced by Koskimies (1957), the development of positive associations between Oldsquaws and Arctic Terns could be attributed to the active selection of tern colonies by Oldsquaws that have been imprinted, as ducklings, to terns that were present in the vicinity of their nest. At Churchill, it was evident that opportunities for auditory or visual imprinting of Oldsquaw ducklings to Arctic Terns typically occurred at hatching. The extent to which such imprinting might influence subsequent choice of nest site by the ducks remains problematical, however, in part due to the early arrival of the Oldsquaw, which may precede the arrival of the terns on the breeding grounds (Taverner and Sutton, 1934). In addition, in at least six instances in 1968, Oldsquaws at Churchill had laid clutches prior to the onset of laying by terns on the same islands.

A possible supplement to the imprinting hypothesis was suggested by observations at Churchill of Oldsquaw nest cups, remaining from previous years, on the islands in fresh-water ponds. These old nests, which numbered as high as 10 on a single island measuring no more than 10 by 5 m in size, indicate that, like the Arctic Tern (Cullen, 1956), Oldsquaws may use traditional nesting areas from year to year. Where this tendency is prevalent, then once a nesting Oldsquaw became established in or near a tern colony, association in the same area would be perpetuated in subsequent years regardless of which species commenced nesting first in any particular year. The initial association, according to this interpretation, could presumably arise either as a chance result of similar habitat preferences of the two species or as a result of imprinting.

According to evidence reviewed by Hilden (1965:68) fidelity to a traditional nest site is more likely to occur in the absence of nest disturbance or predation. If true for Oldsquaws, then nests located away from tern colonies, if destroyed by predators, would tend to be shifted to a different location in the following year, whereas those located in tern colonies, where predation is less likely, would tend to be placed in the same location in subsequent years. Such differential predation and nest site fidelity cannot therefore be excluded

as a possible additional mechanism favoring the accretion of Oldsquaw nests in or near tern colonies.

If imprinting alone constituted the proximate cause of associations between Oldsquaws and Arctic Terns, a more or less random distribution of local areas in which associations do or do not occur would be expected. In particular, it would not be expected that the occurrence of associations would necessarily be concentrated in those areas where avian nest predators are locally abundant. According to the alternative view, that associations may be initiated either by similar habitat preferences or imprinting, but are then favored by the tendency of Oldsquaws to use traditional nest sites that are protected from nest predators by Arctic Terns, maximum association in areas where nest predators are abundant would be expected. Further investigations of association between these species, with particular reference to the presence or absence of local populations of avian nest predators, should therefore provide information as to the relative importance of these various mechanisms, all of which must be considered tenable on the basis of existing data.

SUMMARY

A high incidence of nest association between Arctic Terns and Oldsquaws was found at Churchill, Manitoba, in 1967 and 1968. Distances between nests of these species averaged only 2.3 m on islands in fresh-water ponds, increased to an average of 13 m on mainland beach sites, and reached 72 m on mainland tundra.

Potential avian predators of Oldsquaw eggs included the Herring Gull, Parasitic Jaeger, and Common Raven. Clutches lost to predators did not exceed a maximum of five of 28 nests observed. Observations of Arctic Terns attacking potential predators suggested that Oldsquaws derived protection from nearby terns. It is suggested that such protection, coupled with a tendency to return to successful nest sites in successive years, affords a possible supplement to habitat preferences and imprinting of ducks to terns as the proximate mechanism responsible for the maintenance of nest associations between these species.

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SEASONAL CHANGES IN FLOCKING BEHAVIOR OF STARLINGS AS CORRELATED WITH GONADAL DEVELOPMENT

G. JAMES DAVIS

THIS paper presents data on the seasonal variation in population and flocking behavior in Starlings (*Sturnus vulgaris*) as correlated with gonadal changes. Most research of Starlings has considered specifically the breeding biology (Kliujver, 1933; Marples, 1936; Bullough, 1942; Kessel, 1957; and Collins and deVos, 1966) or the aggregations of Starlings (Wynne-Edwards, 1929; Brown, 1946; Davis, 1955; and Jumber, 1956) with little attention focused on the relationship between the two. With the aid of four weekly census routes to determine the extent of seasonal variation in Starling population and flocking behavior, the relation between the flocking behavior of Starlings and the reproductive cycle is presented.

MATERIALS AND METHODS

Most data were collected in McDonough County, Illinois between 27 June 1965, and 25 June 1966, from four, 25-mile census routes designed to include the four predominant ecological-land use patterns in west-central Illinois. One census route was located such that over 90 per cent of the land adjacent to the road was intensively farmed; the predominant soil type was dark silt loam. A second route was located where 39 per cent of the land was under cultivation while the remainder was composed of oak-hickory forest or woodlots and bluegrass pastures situated on a silty clay loam soil. The other two routes represented situations intermediate to that for the two routes described above. Each route was covered once a week by automobile driven at 25 miles per hour beginning 30 minutes after sunrise. Censuses included only those Starlings located within a 100 yard radius of the car. If possible, censuses were not taken on days when visibility was poor or when it was raining at the starting time as these conditions usually caused counts to be lower than on clear days at the same time of year. Starlings observed along the routes were recorded as to number, activity, adjacent cover, relationship to farm complexes and location on the transect. Starlings were recorded as perching if sitting above ground level and not engaged in feeding activity. Any Starling sitting on the ground was recorded as feeding. Flying was the third type of general activity recorded. Weather conditions at the time of each observation also were recorded. Supplementary data were obtained from 28 morning and 55 evening observations of Starling activity at communal roosts in the Macomb, Illinois area between 10 July 1965, and 28 October 1965, and by random observations of Starlings throughout the study.

RESULTS AND DISCUSSION

Annual Changes in Population Levels.—As reported by many workers (Marples, 1936; McAtee, 1940; Ball, 1945; and Kessel, 1957) recently fledged Starlings occur in flocks varying in size from five to over 300 birds



FIG. 1. The numbers of Starlings observed per 100 miles on four, 25-mile census routes each of which was driven once a week from 27 June 1965, through 25 June 1966, McDonough County, Illinois.

throughout June. During late June formation of juvenile flocks caused the census counts to increase from 150 birds to over 300 birds per 100 miles (Fig. 1). However, from 3 July through 24 July few Starling flocks, adult or juvenile, were observed and counts along the census routes declined to about 100 birds per 100 miles—one of the lowest levels of the study (Fig. 1).

There are few data in the literature concerning observations of Starlings during July which I interpreted as reflecting this low level of Starling activity in July. Random observations of Starling flocks by the author during July and August, 1967, and June and July, 1968, near Madison, Wisconsin further supported the hypothesis that Starling activity is at one of the lowest levels of the year in July. A possible explanation for this low population density and low level of activity in July is that the young birds migrate northward from the general area where they were fledged. Niethammer (1937) reported such movements in Switzerland where young Starlings migrated to the vicinity of the North Sea soon after the juvenile flocks formed. An alternative hypothesis is that the low numbers observed in July are a mani-

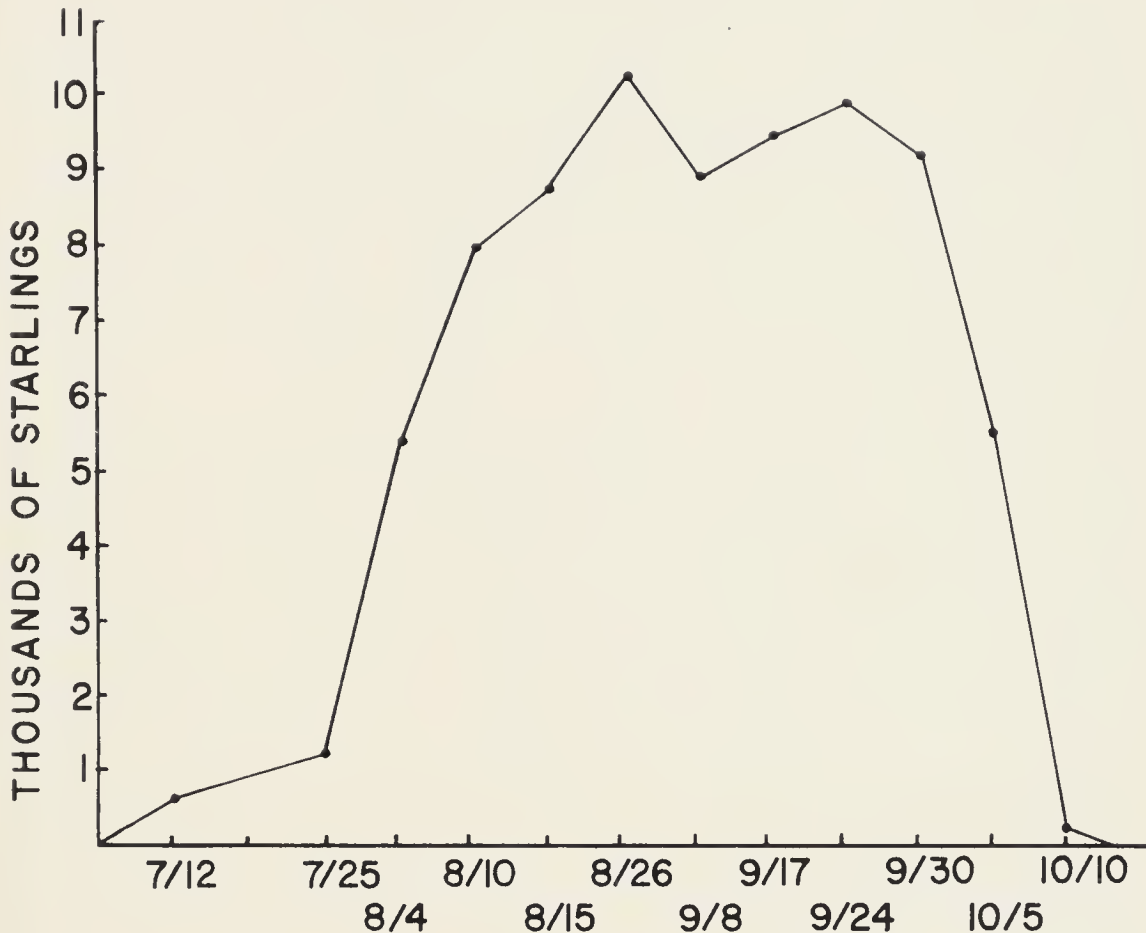


FIG. 2. Numbers of Starlings observed at communal roosts near Macomb, Illinois, during the period 12 July 1965, through 10 October 1965.

festation of the initial stages of summer molt. According to Kessel (1957) the postjuvinal molt of Starlings begins four to six weeks after the young birds have been fledged. Therefore, in Holland (Kluijver, 1933), New York (Kessel, 1957), Ontario (Collins and deVos, 1966), as well as Illinois (Davis, 1966) the postjuvinal molt for the first brood would begin in the early part of July, the period corresponding with the observed decrease in numbers seen during July in Illinois and Wisconsin (Fig. 1). Presumably while molting Starlings are less active and so are less conspicuous to the observer, and their behavior might be of a more secretive nature during this time.

Following these periods of low populations Starling numbers recorded increased gradually and by 21 August a level of 275 birds per 100 miles was recorded (Fig. 1). After 21 August the numbers increased rapidly to about 800 birds per 100 miles and remained at that level from 20 September through 9 October (Fig. 1). During August and September in the Macomb area the number of communally roosting Starlings also increased rapidly to the highest level recorded for the study. By late August numerous small flocks using

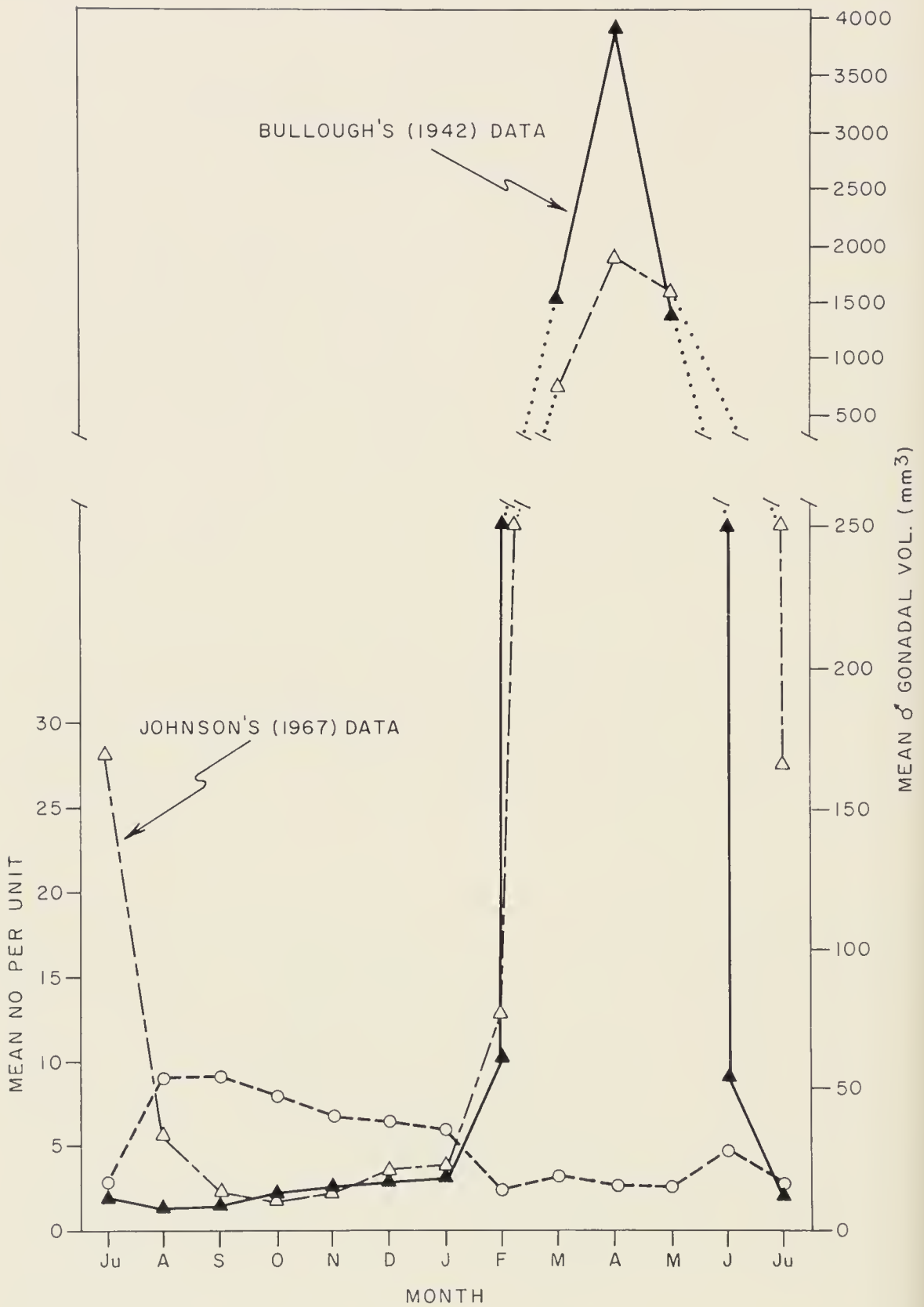


FIG. 3. The average Starling flock size, by monthly periods, observed on four 25-mile census routes each of which was driven once a week from 27 June 1965, through 25 June 1966, in McDonough County, Illinois in relation to average monthly volume of Starling testes as adopted from Bullough (1942) and Johnson (1967).

temporary roosts had consolidated into one large flock using a single communal roost (Fig. 2). The tendency of Starlings to aggregate was noticeable in the census counts, for as the population increased through August the number of individual flocks observed decreased from 45 per 100 miles (25 July through 31 July) to 27 per 100 miles (15 August through 21 August). This late summer change in flocking behavior is reflected more dramatically in the average flock size which was two and one-half birds in July while in August, the average flock size had increased to over eight birds per flock (Fig. 3).

From these results it would appear that the southward migration of the northern adult Starling populations began as soon as August flocking occurred. Bullough (1942) after completing a study on the reproductive cycles of British and Continental Starlings concluded that sex hormones in the blood inhibited fall migration (Fig. 3). He believed that as the gonads decreased in size, reaching their smallest size in July and August, the amount of sex hormone released into the blood decreases and the birds are induced to migrate southward. Once Starlings begin southward migration they are thought to travel slowly and leisurely along definite routes.

A few banding returns from west-central Illinois suggest that Starlings migrate into and out of west-central Illinois by two different routes; one to the northeast along the Illinois River and along either side of Lake Michigan and the other along the Mississippi River (C. Martin, unpubl. data). The west-central Illinois study area is situated midway between these two flyways and so, the period of maximum population density, 20 September through 9 October (Fig. 1), probably represents the convergence of migrating Starlings from these two migration paths. These migrating birds appear to remain in the west-central Illinois area through September as a settled population feeding throughout the day in large flocks in hog and cattle pastures, and roosting communally at night.

This period of high population density, 20 September through 9 October, was followed by a sudden decrease in the Starling population to about 400 birds per 100 miles of census route, which in turn was followed by a marked increase to about 800 Starlings per 100 miles during the week of 18 October through 24 October (Fig. 1). The following week of 25 October through 31 October, the Starling population again returned to a level of 400 birds per 100 miles. Throughout this entire period, 10 October through 31 October, no large feeding flocks or communally roosting Starlings were observed in the Macomb area (Fig. 2).

The sudden decrease in population which occurred during the week 10 October through 17 October is thought to be the result of most of the adult population migrating southward from the west-central Illinois area because

of food shortage and cooler fall temperatures. A possible explanation for the second peak in population density during the period 18 October through 24 October is that young Starlings were migrating through the area after the adults already had migrated. As stated previously, Niethammer (1937) reported northward movement by juvenile Starlings after fledging. Because of this summer movement northward, he suggested that young birds would migrate south later than the adults. This hypothesis is further supported by the observations in Illinois that during this second period of high population density no communal roosts were found in the west-central Illinois area and flying Starlings constituted a larger proportion of the censused population than at any other time of the study (Figs. 1 and 2). The data indicate that these Starlings were passing through the area rather quickly.

During the period November through February, Starlings remaining in the area for the winter were observed roosting only in small groups in natural cavities and buildings and they fed nomadically throughout the day near cattle and hog feedlots or refuse areas. Census counts throughout the winter fluctuated with weather conditions; i.e., severe winds or cold temperatures made the birds less active and thus less conspicuous to the observer resulting in lower census counts (19 December through 25 December and 26 January through 1 February). During the colder part of the winter, 13 December through 26 February census counts dropped 48.1 per cent to slightly over 100 Starlings per 100 miles (Fig. 1).

Part of the observed winter decrease in Starling numbers can be interpreted as winter mortality which according to Kessel (1957) is nearly 25 per cent of the spring population. However, most of the observed decrease in Starling population during the winter is thought to have been the result of "weather movements," i.e., when increasingly cooler temperatures occurred in an area birds migrated to warmer climates and to a more available food supply.

During February the average flock size decreased from over 6.5 birds per flock to near 2.5 birds per flock (Fig. 3). At this time Starlings began showing an interest in potential nest sites as also observed by Kluijver (1933), Marples (1936) and Kessel (1957). During the period 27 February through 6 March, the first signs of additional birds migrating into west-central Illinois were observed as population levels increased from 120 birds per 100 miles to over 300 Starlings per 100 miles of census route (Fig. 1).

These February observations are difficult to interpret. The interest shown by the permanent residents in potential nest sites is believed to be the effect of rapidly increasing gonadal activity preceding the approaching nesting season (Bissonette and Chapnick, 1930 and Bullough, 1942). Bullough (1942) in his study of reproductive cycles of Starlings (Fig. 3) concluded that the

increase in gonadal activity in February caused higher levels of sex hormones in the blood which stimulated the Starlings to migrate in the spring (Fig. 3). Spring migration is accomplished in a different manner than fall migration (Fig. 1). Spring migration in France (Quepat, 1874) and New York (Kessel, 1957) also occurred in the first part of March. Szmironov (1929-30) reported the rate of spring migration in Finland and South Russia was 32 miles per day. If Starlings migrate in Illinois at the rate of 32 miles a day, it seems probable that Starlings migrate in a less gregarious manner and over a longer period of time in the spring than in the fall since spring migration did not show dramatic increase of Starling population or the large flocks associated with fall migration (Fig. 1).

Through March and April the Starling population in west-central Illinois remained at between 250 and 300 birds per 100 miles of census route, even though Starlings still were migrating through the area (Fig. 1). The spring population is composed of two distinct Starling groups, the nesting population and the nonbreeding or migratory population. The nesting population always was near potential nest sites, perching, displaying, or building nests. The nonbreeding or migratory population showing only slight gonadal activity (Johnson, 1967) occurred in small flocks flying in open fields or perched near farm feedlots.

After spring migration and during the height of the nesting season, 20 April through 26 May, the Starling population as determined from the census routes, was low, or about 100 birds per 100 miles of census routes (Fig. 1). The number of Starlings did not increase appreciably until after the fledged young of the first brood were being observed in late May and throughout June. Then Starling population levels increased to over 250 birds per 100 miles during the last week of the census, 19 June through 25 June.

The decline in population during the nesting season can be attributed to the fact that one half of the adults were at the nest sites incubating eggs or brooding the young and could not be observed during the census. The gradual increase in population in May and June was the result of first family units being observed (Marples, 1936) and later the formation of the juvenile flocks (Kessel, 1957).

Flocking Behavior.—The flocking behavior of Starlings is distinctly different in two periods of the year: there is a 6-month period during which there is a tendency to flock and a 6-month period during which there is almost no tendency to flock (Fig. 3). During August, 1965, the average flock size increased suddenly from 2.5 birds per flock to nearly 8 birds per flock. Then for the next five months the average flock size decreased gradually until January when the average was about 6.5 birds per unit. In February the average flock size fell sharply to 2.5 Starlings per flock where it re-

mained through July, except for a slight increase in average flock size during June resulting from the formation of juvenile Starling flocks (Fig 3).

If gonadal volume of male Starlings of the west-central Illinois population (Johnson, 1967) and an English population (Bullough, 1942) are plotted in relation to the average monthly flock size as determined by the census routes in this study (Fig. 3), it appears that as the gonadal size increases (which is a general indicator of the amount of sex hormone produced) average flock size decreased. I suggest that the tendency to flock among Starlings is inversely related to the level of sex hormones in the blood. This is further supported by observations in the spring that flocking birds show little or no gonadal development (Kessel, 1957).

SUMMARY

1) Starling populations in west-central Illinois dropped to one of its lowest levels of the year in July 1965 (100 birds per 100 miles of census route) as a result of either young Starlings migrating northward or the postjuvinal molt making the Starlings less active flyers and less conspicuous to the observer.

2) The initial stages of migration were observed in August as the average flock size increased from 2.5 birds per unit to over 8 birds per unit. From this time the Starlings began to accumulate until populations reached a peak of over 800 Starlings per 100 miles of census route during the period 26 September through 2 October.

3) The migration from further north of young Starlings through west-central Illinois after the adults already had migrated through was thought to be the cause of a second peak in the population to nearly 800 birds per 100 miles of census route in late October.

4) Starling populations gradually declined over the winter from 250 birds per 100 miles to about 100 birds per 100 miles of census route as a result of "weather movements."

5) In late February the average flock size decreased from 6.5 to 2.5 birds per unit as some Starlings began showing an interest in potential nest sites.

6) Spring migration into west-central Illinois which began in the first week of March did not exhibit the large flocking tendency of fall migration and it occurred over a longer period of time.

7) During the nesting season the numbers of Starlings observed along the census routes were low, about 100 birds per 100 miles of census route, because the adults were confined to the vicinity of the nest by nesting activities. The numbers along the census routes did not increase again until June when the fledged young formed into juvenile flocks, and the counts rose to near 300 birds per 100 miles of census route.

8) The flocking of Starlings was of two distinct types: during August through January, there was a tendency to gather into large flocks and during February through July, there was a tendency to occur only in pairs. It is believed that the tendency to flock among Starlings is inhibited by the level of sex hormones in the blood.

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SPATIAL DISORIENTATION IN BIRDS

A. D. HERBERT

THE aircraft was on final approach through the rain and fog. At approximately 500 feet it went into a spiral dive to starboard, striking the right wing against the approach lights. The aircraft was destroyed.

Blackburnian Warblers were migrating on a night of a low ceiling and the visibility restricted in moderate rain. On reaching a floodlighted area, some fifty birds crashed into a hangar and were killed.

Initially there does not seem to be much in common, except the weather, in these two unfortunate occurrences. Yet, under analysis, there may be a great deal of similarity. In both cases the fliers were attempting to fly through deteriorating weather conditions, picking their way through a maze of light and shadow, of reflected and refracted light shining through rain, an opaque obstructing medium. It is suggested that the cause of both the crashes was exactly the same. The fliers became confused by the abruptness of intense lighting, and, using the primary sense of orientation (sight) in conjunction with erroneous sensory stimuli, suffered a complete loss of spatial orientation. Birds, particularly the nocturnal migrants when flying at low level are susceptible to, and suffer from vertigo and spatial disorientation the same as man.

For the purpose of this discourse it is assumed that: (a) the aerodynamic forces acting on the wings of a bird are the same as those acting on the wings of an aircraft; (b) only nocturnal migrants are under consideration; (c) the sense organs are used for the same basic purposes in both birds and man; and (d) while the senses of the bird may be more acute, the psychophysiological reactions to the stimuli are similar in birds and man.

Although the aerial environment is applicable to both birds and man, each has its own peculiar environment in which it flies and this is not readily examinable by direct observation. This environment is made up of stimuli appreciated by sensory organs and perceived by the brain. The reactions to the stimuli are based upon knowledge, and each reaction must be correct in the proper place at the proper time. Because the human pilot is sensitive to similar stimuli, man can visualize the aerial world of other fliers. It is only through a comparison of the bird with man's knowledge of flying that we can deduce how a bird flies.

As spatial disorientation is extremely common (90 per cent incidence) amongst all-weather pilots, the most expedient way of determining the happenings and causes of spatial disorientation in birds is to consider first the human pilot.

THE HUMAN PILOT.

Before discussing the orientation senses in relation to flying, let us review the actions of the senses of orientation governing the locomotory organs. These organs have the sole purpose of propelling the body or appendages in a given direction for a given distance. Under certain circumstances these organs can become useless, as when the governing apparatus, the orientation senses, is impaired in its function. Consider the children's game of Blind-Man's-Buff or Pin-The-Tail. The child is subjected to a mild case of vertigo, or spatial disorientation, and is asked to achieve a specific goal. Although the locomotory organs are functioning perfectly, the orientation senses are impaired causing an erratic approach toward the target. Although the child is subject to gravity, it has difficulty in maintaining a vertical orientation. It is therefore reasonable to conclude that controlled locomotory action is dependent upon spatial orientation.

For the human on the ground, spatial orientation is necessary only within a two dimensional field. The aviator must have a true spatial orientation. He must be capable of determining a three-dimensional move: of assessing his position relative to a fixed object (the runway) and a moving object (another aircraft); and of determining his position relative to the horizon.

Flying on a cloudless day, the pilot is at the center of a vertical hemisphere. When he is straight and level the ground occupies the bottom half of his visual field and the sky the upper half. The pilot can fly a straight line across the ground because he can see where he is going. During a level banked turn, the horizon rotates at the middle of the visual sphere, going up on one side and down on the other. It is interesting to note that the pilot's immediate reaction is to reorient himself by moving his head and body to maintain a proper horizontal and vertical alignment with the horizon. If the pilot increases the bank but maintains a straight course, his orientation senses will inform him of a side-slip. However, if the bank is made in a turn, the acceleration forces may indicate the turn, or something entirely different, depending on the severity and smoothness of the turn and the forces involved. If the pilot exerts a heavy back pressure or forward pressure on the control column, the orientation senses will inform him of accelerations in these directions even to the extent of overriding the forces of straight and level flight. However, the orientation senses are not as acute as vision in their perception of changes in speed and direction.

The discrepancies between the senses (sight and balance) in flight lead to certain orientation problems peculiar to flying. Prior to the development of specialized instrumentation, the pilot had to remain in sight of the ground because there was no means of establishing a horizontal or vertical datum from which to orientate himself. Even today, with modern instrumentation,

pilots are still subject to attacks of vertigo and spatial disorientation, even to the extent of crashing. Studies have shown that disorientation is, almost without exception, the result of normal psychophysiological processes associated with certain characteristics of flight and of the pilot aloft (Clark and Graybiel, 1955). Therefore, disorientation could be considered to be normal in the sense that it is a perceptual process correlated with the sense organs functioning normally in an abnormal environment.

There are certain characteristics peculiar to flight which make orientation in the air more difficult than on the ground: (a) In flight the pilot loses contact with the ground. He lifts himself above the normal visual aids used to maintain a vertical orientation, i.e. trees, buildings, etc., and is forced to use the horizon to maintain the attitude he desires. (b) The pilot must maintain a three-dimensional orientation, direction, distance, and altitude. The pilot must be aware of his spatial position with respect to the horizon, to fixed objects and to moving objects. (c) The pilot must appreciate the unusual physical forces to which he will be subjected. In the air, while still subject to gravity, he is also subject to accelerative forces which may be continuously changing both in magnitude and direction, even to the extent of negating gravity. (d) The speed and altitude of the aircraft impose further stresses on the senses of the pilot. A more acute sense of spatial orientation is required for flight near the ground than at high altitudes. The increase in availability of visual cues closer to the ground may not necessarily increase the ease of orientation; the abundance of cues may, in fact, lead to confusion. Similarly, spatial disorientation at high altitudes may occur because of the greater sparsity of visual cues.

The above is very basically the pilot's problem in maintaining spatial orientation and he must learn to appreciate these problems before he can fly. However, there are additional problems which may impose further stresses: (a) Visual cues may be reduced or be missing entirely. In the air, gravity is a minor cue, and the horizon may be completely obscured. Thus the pilot is forced to use his instruments to obtain a reference to the horizontal. In this situation he has an indication of his attitude, but his relative position to external objects is completely unknown. (b) False cues may be presented to the pilot by natural phenomena outside the aircraft. Cloud formation, precipitation, lights, reflections and refractions of lights, Aurora Borealis, etc., all may cause spatial disorientation. Accelerations may override gravity and be substituted for gravity, particularly if the accelerations are maintained for a prolonged period. (c) The discrepancies which exist between the senses themselves and between the senses and the instruments may be exaggerated when the "G" forces of a tight turn override gravity and indicate the vertical is in the direction of the force while the instruments indicate

the vertical in another direction. There is also the phenomenon of recovering from a turn and still having the impression of being in a turn, although the visual cues belie the sensation.

There are other factors which must be considered. A seemingly minor point, but actually a very important one, is that the vertical axis is usually obtainable only when a horizontal reference is provided while flying. The vertical axis is the predominant one to a person on the ground; yet when flying, it cannot be accurately determined by itself. Therefore, the horizontal axis becomes the predominant axis. The establishment of the horizontal datum is vital to spatial orientation, as all flying is based upon the aircraft's attitude relative to the horizon, not to the vertical.

Graybiel (1951) states, "Visual perception may become inadequate for partial spatial perception due to inadequate perceptual data. There are many causes for this centering around (1) celestial factors such as darkness, brightness of sun etc., (2) atmospheric conditions such as rain, fog, etc., (3) inadequate visual framework and (4) factors relating to the plane such as small size of windows, glare, etc." Another cause can be ground lighting such as street lights, approach lights, floodlighting. While no statistics are available, it is suggested that the majority of the cases of spatial disorientation occur at night. The optimum conditions for spatial disorientation seem to be a night with low cloud and moderate to heavy precipitation, and the aircraft near, (within 2000 feet) or in the base of the cloud. If the aircraft is near any illuminated area, flying becomes a difficult task, because the pilot is subject to sporadic visual cues which are readily misinterpreted. The refracted and reflected surface lighting is coming from angles which are not usually experienced. There is a pronounced diffusion of surface lighting in precipitation similar to the haloes around the sun or moon when seen through cirrus or thin alto-stratus cloud. The horizon is no longer easily identifiable. It is under these circumstances, particularly if the pilot is trying to fly partly with reference to outside visual cues and partly on instruments, that spatial disorientation is most likely to occur.

Armstrong (1952:281) states, "It has been established beyond all doubt that vision is absolutely necessary for aerial equilibrium. If vision is eliminated during flight, all of the other organs of equilibrium have been found inadequate and the pilot becomes hopelessly confused." Davis (1953) states "It is apparent that the normal vestibular apparatus is not sensitive enough for aerial equilibrium and due to the illusion of reversal of motion it may be, under certain circumstances, a distinct hazard to flight." In the light of these two quotations it would appear that the visual sense is the predominant sense of spatial orientation while the vestibular apparatus has a questionable role. Guyton (1961:678-79) states, "In summary, then, the semicircular canals

detect the rate of change of rotation, which is called angular acceleration. The function of the semicircular canals, therefore, could not possibly be to maintain static equilibrium during linear acceleration, or when a person is exposed to steady centrifugal forces." The tactile, visceral, and proprioceptive senses each contribute to the general perception of orientation but are incapable, either individually or in concert, of correctly and exactly orienting the pilot in the air, or interpreting the direction of the forces acting upon him.

A final point to be considered is the background knowledge of the pilot. Graybiel (1951) states, "Spatial orientation may be looked upon as a phenomenon of perception which represents the individual's interpretation of stimuli originating in various organs of special sense." Interpretation of stimuli is the correlation of the visual cues with the other sensory cues. The interpretation must be based on knowledge which is derived either from previous experience or some other source. However, the knowledge used may be very basic or minimal, or it may be based on assumptions of the normal. In attempting to rationalize the situation, the pilot may accept false cues, both visual (physical) and sensory, as true cues and react accordingly. Therefore, under flying conditions which tend to promote spatial disorientation, there must be a conscious reasoning and knowledge of the problems of orientation or complete vertigo and spatial disorientation is the usual result. Restoration of spatial orientation can be achieved only through a correct interpretation of the accepted visual cues.

To summarize, the following two major groups of factors must be accepted:

Physiological Factors.—(1) Sight is the most important sense associated with spatial orientation. (2) The vestibular, tactile, visceral, and proprioceptive senses each contribute a small part of the necessary intelligence to maintain orientation, but these senses are not generally effective, either in concert or individually, and may at times contribute to disorientation. (3) Knowledge and ability to assess both visual (physical) and other sensory cues is essential to maintaining or regaining spatial orientation. Knowledge of the phenomenon itself is vitally important.

Physical Factors.—(1) The loss of visual cues by darkness, precipitation or fog, or any combination thereof; (2) inexperience in flying in such conditions that visual cues are lost; (3) conflict between the cues to orientation. This may be a conflict between visual and other cues, particularly when centrifugal force replaces normal gravity; (4) prolonged turns at a constant speed with rapid recovery to straight and level flight; (5) unusual maneuvers at night; (6) gradually entering any unusual position without being aware of it; (7) sudden accelerations and decelerations at night; and (8) failure of the pilot to constantly recognize his position in the three-dimensional world of flight.



FIG. 1.

THE BIRD

Before proceeding with any analysis of a bird's orientation faculties, let us review a few instances of avian crashes.

In September, 1961, Blackburnian Warblers were migrating through the area of a Royal Canadian Air Force Base. The weather situation was one of low ceilings and restricted visibility in rain. The geographic plan of the station is as shown in Figure 1. The fronts of the hangars (B) were floodlit facing the tarmacs (E). The revolving light beacon (X) on the control tower was in operation. Three hundred yards east the floodlights of the Motor Vehicle section (C) were shining on the parking area (F). The floodlight on both the hangars and the Motor Vehicle section are forty feet above ground on the fronts of the buildings, while the revolving beacon on the tower is 80 feet above ground. The lights from inside the vehicle section were shining through the opaque glass in the doors.

As far as can be ascertained, the birds were flying in a south south-easterly direction as they had been during the previous five nights. Of the five birds which came to grief

against hangar (A), two were on the north end and three on the south end. No birds were found around the control tower (X), and only three along the rest of the hangar line (B). However, 30 birds were found dead in front of the Motor Vehicle section (C) and 23 more were found against a secondary garage (D) 100 yards south of (C). Restricted space could not be a contributing factor as there is unlimited room for the birds to avoid these obstacles. The hangars, (B) are no higher than two-storied structures. Why, then, did these birds fly into the buildings?

Hochbaum (1955) reports a Mr. Don Knox, "We had a week of very foggy weather November 12 to 18 and the trees and fields of stubble were coated with hoar-frost. The sun was hidden for days and at times it was difficult to see more than ten feet ahead in daytime. On the evening of the 15th, Mr. Knox decided that it would be a good time to burn an old straw stack, so set it afire about 7:30 p.m. Next morning as he was driving along the road he noticed a few dead ducks scattered here and there but thought little about them as ducks often strike the telephone lines and kill themselves. A little later he noticed something unusual going on in the stubble field and went to investigate. Mr. Knox was amazed to find hundreds of dead and dying ducks, some with smashed bodies, some with broken legs and wings, and others less seriously injured but apparently dazed and unable to navigate properly."

Baldwin, (1963) states: "In the fall of 1962 at the Long Point Lighthouse, on a night when migrants were swarming around the revolving light, the writer was disturbing warblers, thrushes and sparrows from the long grass at the base of the flood-light tower (a recent innovation) where they had fallen or were resting. Time and again birds would flutter up from the long grass to a height of five or six feet and then fly directly at the white concrete structure."

A report of bird kills around TV towers is contained in a study by Tordoff and Mengel (1956). In their description of the tower they state, "The tower is lighted by a series of red lights, some flashing and others steady." These lights undoubtedly are obstruction warning lights for aircraft. In a further paragraph they note "all major kills at Topeka occurred when the migrating birds encountered either a cold front or a stationary front lying over eastern Kansas. Typically, this frontal weather included rain, fog, and cloud ceilings down as low as 800 to 1000 feet. Weather of this type presumably forces the migrating birds to fly below the cloud ceiling and thus brings them within the altitudinal range of television towers."

Stoddard (1962) cites innumerable examples of birds striking TV towers under similar weather conditions. All these towers must conform to a certain standard of illumination as provided by various aeronautical governing agencies. Why do birds fly into these illuminated obstacles?

Howell (1955) cites examples of birds being killed by ceilometers around airports. He states "that it occurs only when certain factors coincide; these are an overcast of 5000 feet or less, a wind with a velocity of at least five miles an hour from the north, and a large volume of migration. It might be added that these weather conditions are usually associated with a cold front." Amelia Laskey (1956) notes that "On the night of September 24-25, 1955 more than 1400 birds of 51 species were killed or injured at Sewart Air Force Base, Smyrna and a few at Berry Field, Nashville. After a week of warm weather with temperatures reading 90 to 97 degrees, there was a sudden change on September 24. Rain and northerly winds prevailed with temperatures for that day ranging from 73 to 68 degrees. When the rainfall ceased in the afternoon, the cloud ceiling was only 500 feet."

Laskey (1956) reports that "at 9:45 p.m. there were hundreds fluttering rather high in the beam." It is interesting to note Howell (1955) when he states "We concluded

that the probable cause of death was aerial collision between migrants followed by flying or falling against the ground. While we could not report an actual eyewitness account of aerial collision between migrants such collisions have since been witnessed by Capt. R. L. Edwards, at Maxwell Air Force Base, on the night of October 7-8, 1954."

Prior to discussing the physiological make-up of a bird, it is necessary to discuss briefly its mental capacity. Herrick (1924) states, "It is everywhere recognized that birds possess highly complex instinctive endowments and that their intelligence is very limited." Van Tyne and Berger (1959) corroborate this statement of Herrick. A limited knowledge and reasoning ability affects everything the bird does. When a strange situation is forced upon it, the bird cannot rationalize the situation, but employs the trial and error method. If given enough practice the bird will eventually learn to solve the task. However, once the task is learned and time interval between practices increased, the memory or knowledge of the situation fades and the bird again resorts to trial and error.

When the bird is confronted with natural phenomena, it has an adequate mental capability and can adapt itself to meet the changing situation. However, in dealing with unnatural phenomena (i.e. outside electrical lighting, buildings, TV towers, etc.,) the bird does not have the necessary knowledge or the ability to reason. Also these phenomena erupt at a very alarming rate which tend to preclude adaptations. Therefore, the bird with a knowledge of unnatural phenomena or the ability to recognize them, must have a greater facility for reasoning than the present class of Aves, or be hatched in an area where such phenomena are a part of its natural environment (urban dwellers.)

Perhaps the bird is compensated for a lack of mental ability by a highly attuned reflex action and acute visual capability. Mann and Pirie state. "Small birds, hunting for minute seeds and insects also require good eyesight. and it is obvious, both from their way of life and from the structure of their eyes and brains that birds rely on sight more than any other sense except the proprioceptive one." It would seem that the eye of the bird is its basic source of knowledge and the basic sensory organ for its actions. Van Tyne and Berger (1959) classify the eyes as the most important sensing organ of the bird.

The bird is more capable of acute night vision than humans. The author has seen innumerable birds fly out of the beams of headlights and flashlights into the dark. None have ever been seen to crash into any obstruction. It cannot be suggested that the birds are blinded in one eye. If this were the case, the birds would normally maintain a circular flight path but they definitely do not. Therefore, it can be accepted that natural darkness is a phenomenon that the bird is familiar with.

Other sensory organs of bird may be used for spatial orientation. The visceral senses of a bird may be used in flying. A glimpse at a bird, while it is flying, will reveal the silhouette of a high-wing monoplane. The high mounted wing gives a stabilizing advantage through pendulum effect, with the viscera positioned at the bottom of the pendulum. An appreciation of a roll around the bird's fore and aft axis could be realized through its visceral senses. Suppose the bird were flying on a straight course at a constant 45 degrees to the horizontal. The heavier parts of the viscera would tend to realign themselves with gravity. While the movement of the viscera would be slight, it be would appreciated the same as the dispersement of the human viscera on laying down. The realignment of the viscera would be sufficient for the bird to realize that its body is not aligned with gravity. Also, if the bird in level flight suddenly tried a loop or a bunt, the viscera through its slight movement would give an indication of positive or negative "G" loading. Therefore the viscera of a bird can appreciate both accelerations and gravity.

A second means of appreciating a bank would be through the "tactile" senses of the feathers. The weight of a bird while in a bank is still acting through gravity but the lift, generated by the wings, is acting at right angles to the bird's lateral axis. Because the lift no longer balances the weight, the bird will tend to side-slip. The side-slip induces an increased airflow over the lower wing as the airflow is now coming from ahead and below, instead of a straight ahead. The change in direction of airflow causes an increased air pressure against the downward side of the bird's body. The body, because of its inclination, produces a blanking effect against the inclined airflow over the upper wing. The blanking effect produces a decreased lift on the upper wing, and a decreased air pressure against the feathers on the upper side of the body. Thus the bird, by "tactile" sensory perception, can evaluate a comparison of airflow pressures and appreciate the fact that it is flying on an inclined plane.

Did Hochbaum (1955) recognize the "tactile" and visceral senses in his statement: "Not only is the blindfolded bird able to balance its head when held in the hand, but when it is cast into the air, body and head quickly assume the posture of flight. Like a cat falling with its feet to the ground, the blindfolded bird quickly adjusts to its belly-down flight attitude when cast aloft." In the air the bird senses only differential air pressure on its various surfaces and the "G" forces on its viscera. Therefore, the bird, conscious of not sensing its weight on its lower body surfaces against land or water, can only assume that it is in the air. Consequently, it will quickly assume the position of flight, whether right side up or not is of no great importance. The pendulum effect of the body, particularly with a reversed center of gravity, will quickly return the bird to its normal flight attitude.

Also the visceral senses will indicate an abnormal flight attitude. The "tactile" senses of the feathers will also inform the bird of an abnormal attitude. Thus the bird has many stimuli, other than the vestibular apparatus, to re-orient itself. However, the bird was not flying under these circumstances and did not attempt to fly until it was properly oriented.

It is suggested that the bird did not balance its head by use of the vestibular apparatus when cast into the air. When cast into the air, the bird was aware of being in the air. Once this knowledge was realized the bird assumed a flying posture. Through the use of its proprioceptive senses, it realized that it had not assumed the proper posture for flight. The relationship of the head, neck and body in a flight posture is a natural or learned posture, thus the bird readily assumes the posture.

Mann and Pirie (1950) state that "the proprioceptive sense is the sense of passive position and the movement of the body in space." Here again is a relative sensory perception. It is suggested that the proprioceptive perception of visceral movement can indicate a bank and be discerned by the bird. However, the proprioceptive sense is much more important. The proprioceptive sense is generally accepted as a sense of musculature position. A bird can be conscious of flapping, dragging its feet, bending its neck etc., but the knowledge will in no way affect its spatial orientation at the moment. If we reword Mann and Pirie's statement to read "the proprioceptive sense is the sense of movement of the body relative to its passive parts," then the proprioceptive senses may indicate a future spatial orientation. The proprioceptive sense is used to control the bird's posture and govern its airspeed.

The vestibular apparatus is conceded to be the main internally-cued organ of orientation. Thus the position of the vestibular apparatus is of great importance. By analogy, the vestibular apparatus is comparable to the gyro-horizon system of an aircraft. This system must be mounted on a fixed platform although the gyro is allowed its own rigidity in space. The aircraft is then allowed to turn around the gyro. Similarly, the vestibular apparatus is mounted in the head. Hochbaum (1955) makes a point of stating that "this steadiness of the head must be of tremendous importance to a bird's safe arrival from flight, especially in landings made under turbulent conditions or in wooded places. While this stability of the head, regardless of body posture, no doubt serves the visual process during flight, it does not result from the function of the eyes, that is to say, visual orientation alone is not responsible for this balance." Of course Hochbaum is right; the rigidity of the head is maintained by the vestibular apparatus. The only way the bird can maintain a datum for spatial orientation is to maintain a rigidity of the head since it acts as a mounting for the acceleration sensors of the vestibular apparatus. However, the

vestibular apparatus has to be confirmed by some means. The only means of doing this is with the eyes and the horizon.

The vestibular apparatus is sensitive to accelerations, but not to a constant acceleration or a fixed position. Hochbaum (1955) states: "The circle was not invariably the pattern in all hooded tests. Some birds adopted flights that varied widely from the circle but these variations, though individually distinct, always followed a pattern of curves that carried the bird downwind from the starting place." It would appear that the vestibular apparatus is not sufficiently acute to sense minor discrepancies which can be introduced until the bird has no directional control. Therefore, the eyes of the bird have to establish its initial horizontal orientation and then the vestibular apparatus accepts this position as the normal. Any large deviation from this established position is sensed as an acceleration and a deviation from the normal. The bird must constantly recheck its horizontal orientation by visual cues to maintain its spatial orientation. This way the bird maintains its spatial orientation, sensing disturbances to its equilibrium, as far as the head is concerned through its vestibular apparatus; and to its body through the "tactile" sense of its feathers and its visceral senses. It changes its body posture relative to its passive head through its proprioceptive senses to correct sensed accelerations. Thus the bird uses all of its orientative senses to maintain its spatial orientation; but the basic sensory organs are its eyes—from which it received its initial orientation.

FLIGHT CHARACTERISTICS OF THE BIRD

Good weather.—Locomotion towards any definite goal is dependent on the stimulus applied by the goal and the spatial orientation of the subject. Therefore, before a bird will fly, it must have a motivating factor, and "know which way is up." Spatial orientation is necessary even before the bird leaves the ground. No matter how strong the motivating factor is, locomotion in a desired direction is impossible if the bird is not spatially orientated. We have only to watch the pheasant handlers at a dog trial. The handlers get the birds dizzy, or subject to spatial disorientation, and the birds sit where they are put. When the pheasant tries to move, its locomotory organs are not impaired, but its guiding senses cannot effectively control the locomotory organs. The visual senses can determine which way to go and the sight of the keeper and the dog impel action; but, because the pheasant is spatially disorientated, the desired action cannot be achieved. Therefore, it would seem that spatial orientation is a prerequisite to any desired locomotion.

When the bird is on the ground or water, there is an over-abundance of cues for the bird to remain spatially orientated. The weight of the bird itself on its legs gives it an indication of gravitational forces. A glance at the

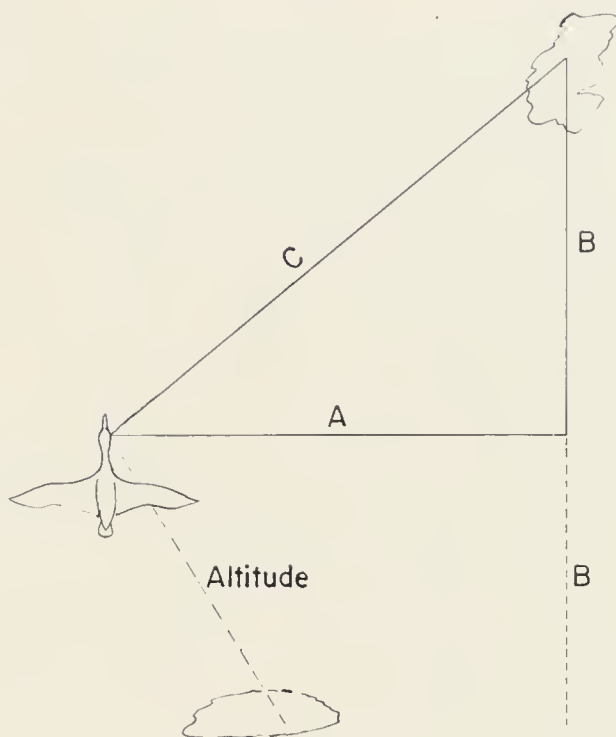


FIG. 2.

surrounding vegetation will determine the vertical. Even when far removed from land, the bird sitting in the water can determine the vertical by its weight on the water surface and the visible horizon. The viscera of the bird is in its normal alignment with gravity. The vestibular apparatus has remained undisturbed by any excessive acceleration. Thus the bird remains well orientated on its land/water environment.

As the bird leaves its land/water environment, it is properly orientated to the vertical and horizontal axes by its gravitational, visceral, vestibular, and visual senses. The first three provide enough stability for the bird to maintain a co-ordinated climb until the transition is made to a horizontal orientation from the vertical orientation.

In the air, the bird must have true spatial orientation. It must be able to determine a three-dimensional move (Fig. 2). The bird must be aware of its altitude, the lateral displacement of its objective (A), the forward or rearward displacement of its objective (B), and the desired route to achieve the objective (C). The bird must also be capable of assessing its position in space relative to fixed objects, to moving objects in space as well as on the ground, and to the horizon. These are the very same problems which confront the human pilot.

On a clear day with good visibility orientation is no particular problem. The bird is flying at the center of its sphere of vision. As Hochbaum (1955)

states, the horizon is always at eye level. Therefore, the upper half of the bird's visual sphere will be sky and the lower half ground. During straight and level flight, these hemispheres of ground and sky will be maintained. When the bird banks to turn, it inclines its head and body to the horizon. This action is not to be confused with the body oscillations of an approach to landing. In our case, the downward eye will have an increased amount of ground visible when the upper eye will have less. Thus the bird has a visual comparison to evaluate its spatial position. The accelerations produced by the turn could be sensed by the vestibular apparatus. However, unless the roll or bank was exceedingly abrupt, it is doubtful if the bird would appreciate the vestibular accelerations. As Queeny (1947) demonstrates, ducks use the eyes as the primary organs of orientation even during such maneuvers as a stall-turn. A glance at the horizon confirms the roll or bank. When the bird wishes to resume straight and level flight, it uses its eyes to re-orient its head to the horizon. The proprioceptive senses then realign the body with reference to the head and level flight is resumed. Finally, the vestibular apparatus realigns itself to the primary axes.

It is submitted that the vestibular apparatus is not as important as has been previously suggested nor is it exact in its perceptions of accelerations. Ducks can be observed turning their heads through many planes while flying, even to the extent of looking backwards, yet no deviations of their flight paths are noticed. The bird is still able to maintain its flight path by the use of its senses and its latent flying ability. Therefore, it is suggested, the accelerations which affect the vestibular apparatus must be strong enough to affect the other orientation senses, excluding the visual sense. However, any sensual perception of acceleration, whether tactile, visceral or vestibular, is immediately confirmed by the eyes.

When the bird encounters turbulence, its whole body and head become subjected to various accelerations. The predominant sense is very difficult to suggest. A straight vertical displacement of the bird would probably be appreciated more by the visceral and tactile senses rather than the vestibular. A horizontal displacement would be appreciated by the visceral and vestibular senses. However, it is unlikely that a straight line displacement would occur because of the bird's inertia. Therefore, a varying percentage of each sense would be appreciated. However, the bird can still see the horizon, evaluate what is happening and reorient itself accordingly.

During its descent for a landing, the bird must reverse the previous transition of orientation cues. Initially the bird selects a general landing area while using a horizontal orientation datum. The bird must continuously assess its groundspeed and track to the landing points; its flight course and the wind velocity; the rate of descent and airspeed; the approach angle

to the landing area and any obstructions; and the changing distance to the landing point. The bird must also maintain an awareness of its spatial orientation (relative to the horizon) and its postural position.

As has been previously explained the postural position is determined through the proprioceptive senses. The postural position of the bird is the basic determinant of the bird's airspeed. Therefore, it must have positive knowledge of its body position. However, its airspeed is sensed by the tactile acuteness of the feathers and the alula. Van Tyne and Berger (1959) state, "The presence of wing slots increases lift which is needed especially at the take-off. The alula functions as a wing slot when it is drawn forward away from the rest of the hand." By inference a bird needs a high lift capacity when flying at low airspeeds. Therefore, the bird's airspeed is determined by its proprioceptive senses and the tactile senses of the feathers.

The vestibular apparatus is needed to maintain a proper vertical and horizontal orientation of the head. Only by maintaining a constantly level head can the changing angles and vectors of a descent and landing be assessed. The bird is also making a visual transition of horizontally orientated relatively high level flight to a vertically orientated low level flight. However, the transition is being done in much less time and with a greater need for accuracy. The bird subconsciously appreciates a general vertical orientation from the overhead light, but this is not accurate enough for landing. The bird's eyes can give the vestibular apparatus a datum, but not continuous information. Therefore, to maintain its spatial orientation, the bird must maintain its head in a fixed position relative to the horizon which the vestibular apparatus is trying to do.

The eyes are busily engaged in assessing the vectors of a descent and landing, since these factors can only be determined through the bird's eyes. It has no other way of gaining the required information for a successful landing.

In summary, flying during good weather is relatively easy for the bird. The bird is flying at the center of its visual sphere. By using its eyes the bird can visually assess its attitude relative to the horizon. However, the bird can assess only the position of its head. The postural position and wing position must be done through its proprioceptive senses. Accelerations from outside the body are sensed through the viscera, vestibular apparatus, and the tactile senses of the feathers. The airspeed of the bird is sensed by the tactile sense and the alula, but it is governed by the posture of the bird. The steadiness of the head is imperative on landing. Only if the head is maintained in a fixed plane can the eyes give a proper recording of the changing vectors. The vestibular apparatus must be able to maintain a rigidity in space of the head comparable to a gyro. However, the regulatory organs for

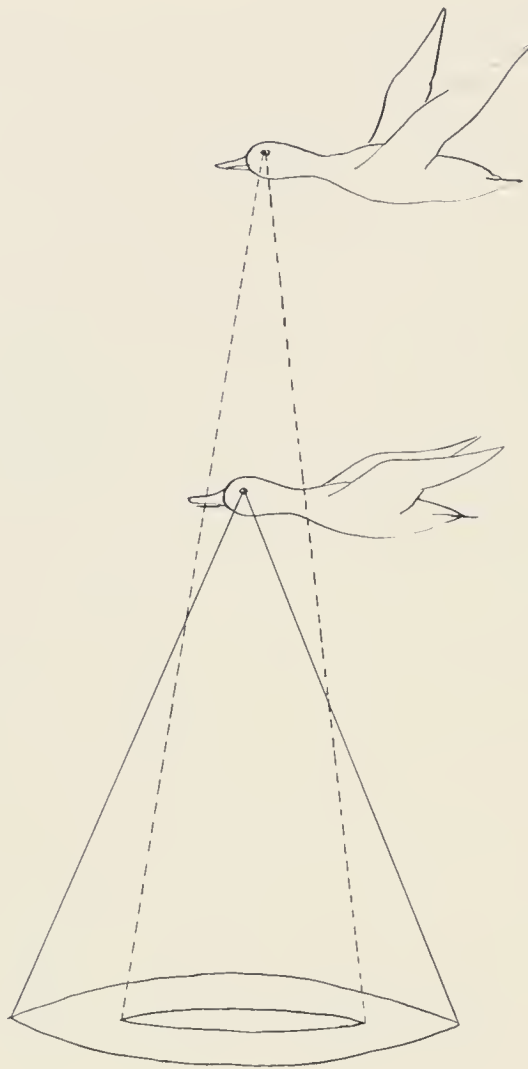


FIG. 3.

the vestibular apparatus are the eyes, as only the eyes can give instant recognition of the vertical and horizontal axes.

Poor weather.—The weather situations which bring about restricted visibilities are low ceilings with precipitation, and/or fog. Flight through restricted visibilities from any cause is exactly the same, except that fog may arrest any but purely local movement.

The bird is forced to reduce its flight altitude to that which will afford a safe passage. As many a marsh hunter has experienced, ducks will and do move in the fog, but at very low altitudes. The visible horizon is the restrictive factor forcing the bird to fly low. Whereas in good visibility the bird was flying at the center of its visual sphere, in poor visibility it is flying at the apex of its visual cone. The periphery of the cone's base is the radial horizontal visibility, or less. The altitude of the bird, or the apex of the cone is de-

terminated by the radial visibility, the bird's speed and its reaction time, not by the vertical visibility. As altitude is increased, the horizontal visibility decreases until the bird can only see straight down.

As the bird requires initiating cues for the vestibular apparatus it must fly at an altitude where it can see a horizon. Therefore an acute cone must be changed to a cone with the largest base. Consequently the bird will fly at a much lower altitude in order to extend its visible horizon (Fig. 3). Also by flying at a low altitude the bird has extended its required reaction time for its airspeed by increasing the visibility distance. It must be remembered that the bird may be theoretically still flying within its sphere of vision limited by the obscuring medium; but this is of no consequence unless something is visible within the sphere.

The method of spatial orientation used by a bird flying through adverse weather is exactly the same as when flying in good weather. The visual sense must provide the datum for spatial orientation. The vestibular apparatus accepts these axes as the datum and senses any deviation. However, the bird sets weather minima below which it will not fly because it cannot maintain its spatial orientation, and its reaction time at its airspeed is too great for a particular visibility.

Nocturnal flight is conducted in exactly the same manner as diurnal flight. The weather will have exactly the same effect on the bird's flight during nocturnal periods as diurnal periods. The bird is faced with exactly the same problems, but they may be of greater intensity because of darkness. However, as Hochbaum quotes Lincoln (1950) "the nights are rarely so dark that all terrestrial objects are totally obscured, and such features as coastlines and rivers are just those that are most likely to be seen in the faintest light, particularly by the acute vision of the bird and its aerial point of observation." Thus darkness is not an inhibiting factor to nocturnal travel but may be a restrictive factor as far as altitude is concerned.

ANALYSIS OF CASES

Let us now apply our knowledge of how a bird flies to the cases previously described when the birds were flying under conditions of poor visibilities and low ceilings and unnatural phenomena. Until reaching the lighted areas, the birds had been flying over the open countryside at an altitude high enough to maintain adequate visual cues for spatial orientation, yet below their normal cruising altitudes in clear weather. Suddenly they were surrounded by lights of various and varying intensities with shadows at a variety of angles. The birds used their knowledge in an attempt to orient themselves and escape from the area. However, their knowledge was of natural, rather than unnatural, phenomena. Such reorientation, based on natural phenomena applied to unnatural phenomena is the initial step toward spatial disorientation.

Consider the first situation—the Blackburnian Warblers flying into the light and shadow. The shadow line from the flood lights extends out from the building at an angle of thirty degrees below the horizontal. Prior to entering the area the bird had been using the natural shadows, the land shadow against the horizon, for spatial orientation. As it approaches the area, the lights are above or level with it and to one side of it. There is also reflected light from the adjacent buildings. The closer the bird approaches the lights, the more defined the shadows become and the natural horizon becomes more diffuse until it fades completely. Having lost its natural datum for orientation, the bird seeks new visual cues in the lights and shadows of the artificial situation. What the bird sees it accepts as true because of its lack of knowledge. Accepting erroneous visual cues, the bird re-orientes itself to the false horizon. Having rolled to a plane inclined from the true horizontal but parallel to the false horizon, the bird attempts to fly straight and level. The vestibular apparatus appreciated and accepted the roll to the new position. However, the roll was appreciated as an acceleration to a new position rather than a return to equilibrium. The visceral senses also show a displacement from the true horizontal or vertical. Now the bird has discrepant cues (visual and sensory) to the horizontal. As the bird maintains the bank it will start a descending turn. The “tactile” senses of the feathers and the pendulum effect of the bird’s body inform it of an incipient spiral dive. As the bird’s brain notes the incipient dive, it starts to take normal corrective reactions; but these reactions do not achieve the anticipated results because the corrective action is to a false horizon. These correct results, according to the inclined plane, promote further accelerations which confuse the bird. The bird is attempting to correlate compounding sensual information with visual information. As will be noted, it is the bird’s inability to analyse the visual and sensory cues that is the basic cause of spatial disorientation. Unfortunately spatial disorientation, when flying, is a phenomenon which occurs with lightning rapidity.

In the case of Baldwin’s observations of the bird flying directly into the lights, the situation is slightly different. The situation is a case of straight loss of visual cues. This situation is analogous to the poacher with his strong light after pheasant. The pheasant remains perched in the light without moving, not because of hypnosis, but because it has lost its visual cues to spatial orientation. The proprioceptive, vestibular, and visceral senses maintain the pheasant’s balance on the tree, but it is afraid to fly because it cannot resolve the problem of spatial orientation without visual cues. The light has obliterated any background and consequently all the pheasant can see is the light. This is exactly what happens when the bird flies into the lights. It loses its visual cues to the horizontal. The vestibular apparatus can measure

only accelerations and when they stop, but not when the bird returns to the normal position. Consequently, the bird is comparing sensory information with visual information and is unable to resolve the problem because there is no visual information. In this particular case it is quite conceivable that spatial disorientation does not occur until such times as the bird takes evasive or corrective action. At that time the vestibular apparatus would be subjected to accelerations. Once the accelerations are reduced to zero the bird has no indication of the true horizontal except tactile and visceral senses, and these senses are not accurate enough for flying. Therefore, with an absence of visual cues, the bird has no means of orienting itself and is forced to accept any cues it can find. If the lights or the shadows are used as a datum, spatial disorientation is the inevitable result.

The refracted and reflected electric light in precipitation produces the same result. With the sun or moon shining on a reflected surface, the bird can maintain a constant bearing or azimuth and angular altitude to the reflected image. (Celestial light is, for practical purposes, made up of parallel rays). However, when the bird attempts this normal reaction with the unnatural light, it immediately begins to fly a curve, because the unnatural light is disseminated radially from its source. Thus the visual senses appreciate a fixed horizon, but the sensory apparatuses appreciate the accelerations of the arc of the flight path. There is a tendency for the rate of turn to increase thereby compounding the accelerations. As the rate of turn increases, there is a change in the angular altitude of the light. To offset the change the bird would have to change its degree of roll thereby producing further accelerations. Now the bird has a visual cue to the horizontal and discrepant sensory cues. Since it cannot resolve the information, it becomes spatially disorientated.

The refracted and reflected light in precipitation produce the same results through exactly the same causes. Because it has a very localized source this light is not directly overhead, but at any angle between the bird and the source of light. This angle is dependent on the proximity of the bird to the source of light. Whether the bird is misled into reasoning that the light is the Aurora or halation from high clouds, is unknown. The bird, however, accepts the light as the true horizon and reorients itself accordingly. The sensory apparatus detects the accelerations. As soon as a comparison of visual and sensory cues is effected, spatial disorientation is imminent. An analysis of the weather conditions in Stoddard's report (1962) will show that on all of the twenty-four occasions, parts of the TV tower were obscured on thirteen nights, the tower was clear on nine nights but there was precipitation on five of these nights. There is no comment on the tower for two occasions. A

further observation from this report is that an halation ring did develop in low cloud and Scotch mist. In these cases the birds have no horizon as a visual cue to the horizontal whether proceeding to or from the tower and are consequently subjected to spatial disorientation through the same causes as previously illustrated.

In the case of airport ceilometers it is evident that the birds are suffering from spatial disorientation, if not complete vertigo, as Laskey (1956) reports "hundreds fluttering high in the beam." In this situation, the intense lighting is from underneath with darkness on top. The lighting situation is the exact reverse of normal natural light. The ceilometer has obliterated any horizon which the birds had prior to entering the light beam. Therefore the only cues it has are its sensory mechanisms plus its sight. As it attempts to reorient itself by sight, the senses appreciate the deviation from the horizontal and the birds become disoriented. Howell's (1955) conclusions as to the probable causes of death being an impact with the ground would substantiate an inability of the bird to orient itself. It must be noted that very few birds collide in the air and fall to the ground. Birds are capable of regaining flight within a foot vertically of the point of collision. If the bird was not disoriented, no spiral dive and ground impact would occur. As such collisions have been witnessed (Howell, 1955), it must be concluded that the birds were unable to take evasive action, and therefore must have become disoriented.

SUMMARY

The bird possesses various senses to determine its spatial orientation. The visceral senses give the bird an indication of its body position in space and of the "G" forces acting upon its body during aerial gyrations. The "tactile" senses of the feathers will give the bird an indication of the airflow pressures on either side of its body and wings and allow the bird to sense a bank or a spiral dive. The proprioceptive senses give the bird an indication of its body position relative to its head. The vestibular apparatus can sense the bird's equilibrium. All of these senses, whether singly or in concert, are not sufficient to maintain a proper spatial orientation. The eyes are the predominant organ of spatial orientation, and for gaining cues to maintain spatial orientation. However, where there are discrepancies between the visual and sensory cues, the visual cues will be accepted rather than the sensory cues. The sensory cues still have sufficient effect to cause a mental block or confusion. The bird has not enough knowledge to analyse the situation and is therefore unable to take any true corrective action. The consequences of the situation is that the bird suffers from spatial disorientation and, in some cases, complete vertigo. The only conclusion is that birds are susceptible and suffer from spatial disorientation, and further that the causes of spatial disorientation in birds are exactly the same as those which affect the human pilot, namely; (a) the loss of true visual cues to the horizontal; (b) inexperience in flying under such conditions where visual cues are lost; (c) conflict between the sensory and visual cues to orientation; (d) entering an unusual position without being aware of it; plus (e) the lack of knowledge and reasoning ability when dealing with unnatural phenomena.

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BREEDING POPULATIONS OF TULE WHITE-FRONTED GEESE IN NORTHWESTERN CANADA

BOB ELGAS

THE Tule White-fronted Goose (*Anser albifrons gambelli*) is one of the least known of the North American wild geese. Available information has been largely limited to observations and collected specimens of wintering birds. The migrational routes are virtually uncharted and breeding areas unknown. The basis for considering *gambelli* to be a valid subspecies is discussed by Swarth and Bryant (1917), Kuroda (1929), Dalgety and Scott (1948), Todd (1950), and Delacour (1954). Reasons for lack of specific information are the comparative rarity of *gambelli*, and the fact it is usually confused with the Pacific White-fronted Goose (*A. a. frontalis*).

Because of the mystery surrounding this goose and the fact it had been listed as possibly endangered by the International Union for the Conservation of Nature and Natural Resources, an expedition to the region of the delta of the MacKenzie River in northwestern Canada was undertaken in 1964. The purpose of the expedition was to try to locate breeding colonies of *A. a. gambelli*, and to collect live birds for a controlled propagation program. Reports that isolated and uninvestigated White-fronted Goose populations nested in this region made it a likely area to search. The expedition, which was originally reported by Elgas (1965), was sponsored and financed by World Wildlife Fund. It was actively supported by the Canadian Wildlife Service, the United States Fish and Wildlife Service and was under the leadership of Bob Elgas and Jack Kiracofe. On 2 July 1964, the expedition arrived at Inuvik, Northwest Territories where a base camp was established. The town of Inuvik is approximately fifty miles east of Aklavik and is on the east side of the MacKenzie River delta. Recognition for his support is given Dick Hill, Manager of the Canadian Wildlife Service Research Laboratory at Inuvik and to Tom Barry, Resident Biologist for the Canadian Wildlife Service. The technical advice and field support given by Mr. Barry was invaluable.

On 5 July we made an aerial examination of the Old Crow Flats. Old Crow Flats is in the northern portion of the Yukon Territory, about 150 miles west of Inuvik. It is a plateau 60 to 70 miles in diameter and rather isolated from the northern coastal plain and the MacKenzie delta area by rugged mountain chains. Here is the source of the Old Crow River. The Flats are characterized by thousands of lakes, sloughs, and potholes surrounded for the most part by a dense brushy growth. Predominant vegetation

TABLE 1

CHARACTERISTICS OF LIVING WHITE-FRONTED GEESE (*ANSER ALBIFRONS*) CAPTURED
IN NORTHWESTERN CANADA, JULY 1964

Specimen Number	Sex	Age When Captured	Chord of Wing (mm)	Exposed Culmen (mm)	Tarsus (mm)	Weight	Color Compared with <i>frontalis</i>
1	♂	Adult	413	57	77	7 lb 11 oz	Darker brown
2	♂	Juvenile	407	56	77	6 lb 9 oz	Intermediate gray-brown
3	♂	Juvenile	405	58	78	7 lb 9 oz	Intermediate gray-brown
4	♂	Yearling	434	58	80	7 lb 2 oz	Darker brown
5	♀	Adult	394	53	78	6 lb 6 oz	Intermediate gray-brown
6	♀	Juvenile	410	49	74	5 lb 6 oz	Darker brown
7	♀	Juvenile	395	49	77	6 lb 9 oz	Darker brown
8	♀	Juvenile	388	54	74	7 lb 2 oz	Darker brown

Nos. 1, 3, 6 and 8 measured 15 February 1968, Nos. 2 and 7 measured 26 November 1964, Nos. 4 and 5 measured September 1965.

consists of spruce, willows, and alders with an undergrowth of various grasses, sedges, and mosses. The "bush" formed a heavy overgrowth condition prevailing virtually to the shoreline of the numerous lakes and ponds. Open, grassy areas were little evident.

Our preliminary search of the Flats revealed few geese, none of which appeared to be breeding birds. We then flew to the village of Old Crow, where we consulted with Charlie Peter Charlie, head man of the village and chief of the Loucheaux Indians. Charlie had spent his entire life in the area and was perhaps more familiar with Old Crow Flats, and its wildlife, than any living man. On a map furnished by the Royal Canadian Mounted Police, Charlie indicated a specific location, in the southwest portion of the Flats, known to his people as Dry Lake, and said we could expect to find breeding White-fronted Geese there. We immediately flew to the suggested location, landed, and spent considerable time in searching the area. While adult and young (breeding) geese were in evidence the heavy brush made observation difficult. We were eventually successful in capturing two downy young Whitefronts, approximately a week old. Unfortunately, a close study of parent birds was not possible since they were not yet in the molt. In flight, however, they appeared larger and darker than examples of *frontalis* with which we were familiar in Alaska. The two downies were darker than any White-fronted goslings I had previously seen. Their distinction from

A. a. frontalis goslings was similar to that of downy *Branta canadensis occidentalis* as compared to downy *B. c. moffitti*. These two goslings, both of which were females, were kept alive for propagation and subsequent study. They are numbers 6 and 7, Table 1.

On 6 July a flight was made from Inuvik eastward to the Kugalik River, about 80 miles distant, where a single White-fronted gosling was taken. This gosling again proved to be a female and was retained for the propagation program (No. 8, Table 1). It was interesting to note that this gosling, which was approximately a week old, was following an adult Lesser Canada Goose (*Branta canadensis parvipes*) and its own parents were not seen. We could but speculate as to the reason, but presumably the gosling had become separated from its own parents and had been adopted by the Lesser Canada. The Kugalik River area was much different from the Old Crow Flats in that a more open and grassier condition existed. Here the willow and alder scrub was replaced by large grassy areas and the contrast between the two conditions was striking. Our time was limited and our visit to the Kugalik was brief, so that our examination of the area was quite inadequate. Presumably other breeding White-fronted Geese may have been utilizing the area and further observation would have been desirable. It was noted that the natal down of the Kugalik River gosling was characterized by the same dark color as the two taken the day before at Old Crow Flats. Downy young Whitefronts reported by Hanson, Queneau, and Scott (1956) from the Perry River, N. W. T. were described as paler rather than darker than *frontalis* downies, and the adults collected there only slightly larger and darker than Alaska specimens.

On 13 July a second trip was made to Old Crow Flats, with headquarters established at the Canadian Wildlife Service cabin at Shafer Lake. This time, banding of White-fronted Geese was undertaken utilizing equipment made available by Tom Barry of the Canadian Wildlife Service. Due to the heavy brush in the Dry Lake area, efforts to band geese there were unsuccessful, although two more downy young were taken (Nos. 2 and 3, Table 1). These two goslings, both males, were approximately two weeks old and were slightly paler than the previously taken young.

Inasmuch as the darkness of plumage of adult *A. a. gambelli* is considered diagnostically significant (Fig. 1) it might be well to again note that the five downies taken by the expedition also displayed a darkness when compared to downy young *A. a. frontalis* of similar age. Downies No. 6 and No. 7 (Table 1), collected at Old Crow Flats and downy No. 8 (Table 1) taken on Kugalik River—all females, were approximately one week old when taken. All three were much darker than downy young of *frontalis* of comparable age. Downies No. 2 and 3 (Table 1), both males, were approximately two



FIG. 1. Captive White-fronted Geese. *Anser albifrons gambelli* in foreground and *Anser albifrons frontalis* in rear. Both are females.

weeks old when taken. Although slightly paler than downies 6, 7 and 8 they were still considerably darker than *frontalis* downies of similar age.

In order to find terrain suitable for trapping geese for banding, it was necessary to move to an area to the eastward where a more open condition existed. Here on the larger lakes, flocks of molting geese were congregated and we were able to trap and band 50 birds. Of these, four have subsequently been recovered, two in Saskatchewan, one in Texas, and one in northcentral Mexico. The geese were captured by utilizing nylon netting which was staked out to form fence-like wings in the water which led into a pound trap on land. The flightless geese were herded into this trap from the water with the float

plane. In the trapping area, which was roughly 30 miles east of Dry Lake, no breeding adult geese or goslings were encountered. It is possible that the adult birds may have come some distance to molt and may not have been representative of the breeding population of the region. Three of these, two adults, Nos. 1 and 5 and a young of the preceding year, No. 4, Table 1, were retained for propagation.

At the end of the field work, the eight live geese were transported to the United States where five, Nos. 1, 2, 3, 6 and 8, have been kept for study by Bob Elgas at Big Timber, Montana, and three, Nos. 4, 5 and 7 by Jack Kiracofe at Boiling Springs, Pa.

MEASUREMENTS

Comparative measurements of Tule and Pacific White-fronted Geese made by David Marshall, Bureau of Sport Fisheries and Wildlife, for field personnel working on the White-fronted Goose study 23 October 1963, from specimens in the Museum of Vertebrate Zoology, University of California, Berkeley, and the California Academy of Sciences, San Francisco:

Anser albifrons gambelli

Adult male (17 specimens)—Wing (chord), 441–480 (451) mm
Exposed culmen, 55–62 (58) mm

Adult female (12 specimens)—Wing (chord), 410–441 (432) mm
Exposed culmen, 49–59 (55) mm

Anser albifrons frontalis

Adult male (28 specimens)—Wing (chord), 391–441 (410) mm
Exposed culmen, 44–55 (50) mm

Adult female (31 specimens)—Wing (chord), 368–419 (400) mm
Exposed culmen, 42–51 (47) mm

Specimens of *Anser a. gambelli* from California in the U. S. National Museum were measured by J. W. Aldrich:

Male—Wing 427, 430, 438, and 452 mm
Culmen 58, 58, 60, 58
Tarsus 79, 82, 86, 81

Female—Wing 425, 401, 410 mm
Culmen 58, 57, 55
Tarsus 79, 79, 76

Adult specimens of *Anser a. frontalis* from Alaska in U. S. National Museum measured by J. W. Aldrich showed ranges and averages of measurements:

Male—(18) Wing 380–425 (404.8) mm
(20) Culmen 46.6–56.5 (51.6) mm
(20) Tarsus 68–81.5 (75.5) mm

Female—(15) Wing 362–405 (387.7) mm
(17) Culmen 46–54 (49.7) mm
(17) Tarsus 66–75 (71.1) mm

WEIGHTS OF ADULT *Anser albifrons*:

After Swarth & Bryant (1917):

- (6) male *Anser a. gambelli* California 7 lb 1 oz-7 lb 8 oz (7 lb 4 oz)
- (2) male *Anser a. frontalis* California 5 lb 0 oz-5 lb 6 oz (5 lb 4 oz)
- (4) female *Anser a. gambelli* California 5 lb 5 oz-7 lb 0 oz (6 lb 5 oz)
- (3) female *Anser a. frontalis* California 3 lb 14 oz-5 lb 8 oz (4 lb 12 oz)

Present study:

- (3) male *A. a. gambelli* Old Crow Flats, Yukon 7 lb 11 oz; 5 lb 12 oz; 7 lb 9 oz
- (2) female *A. a. gambelli* Old Crow Flats, Yukon 5 lb 6 oz; 7 lb 2 oz

After Hanson, Queneou and Scott (1956)

- (2) male *A. a. albifrons* Perry River, N.W.T. 5 lb 10 oz and 6 lb 8 oz

DISCUSSION

It is suggested that the downy young taken at Old Crow Flats should be considered as representative of the Old Crow breeding population. The fact that downy young taken at Old Crow Flats did, upon maturing, develop into adults typical of the race *A. a. gambelli* indicates that, according to observations made by the Elgas-Kiracofe expedition, *gambelli* must be considered the breeding population of that area. It should be further noted that the expedition encountered no small pale breeding birds, *A. a. frontalis*, at Old Crow Flats and the small pale birds encountered were, in each case, nonbreeding molting birds. The mere presence of small pale birds in the breeding area would not necessarily be significant because of the well known tendency of adult nonbreeding geese of one race to wander considerable distances into the breeding grounds of another race.

In comparing the weights and measurements of Old Crow Flats and Kugalik River birds (Table 1) with those of *A. a. frontalis* and *A. a. gambelli* obtained from other sources, it is evident that the exposed culmens of these birds fall well within the range for *gambelli* and closer to the average for this subspecies. Wing (chord) measurements of these birds are small but cannot be satisfactorily compared due to the unusual amount of wear of wing tips which is commonly seen in pen-reared birds. Tarsus measurements are inconclusive. Weights are within the range of *gambelli* and greater than those of *frontalis*. Plumage color is typically darker brown or grey-brown than *frontalis*, as is characteristic of *gambelli*, with the exception of birds 2, 3 and 5, which are midway between the two forms. In combined characters, the Old Crow Flats birds seem to be referable to *gambelli* although they fall in the lower part of the size range of that race as represented by migrant specimens from California. It is possible the average of California specimens is not typical of the subspecies but abnormally high due to selection for large birds by the collectors. Further, it should be recalled that the type specimen

for *gambelli* came from Texas and the California birds may not be as typical of that race as are those from Old Crow Flats.

CONCLUSIONS

It is obvious that the Elgas-Kiracofe expedition in 1964 was unable to undertake as thorough an investigation of the White-fronted Goose populations of the MacKenzie River delta area, as would have been desirable. However, information obtained from the small samples collected, which are known to represent the breeding population of that area, indicates that these birds are referable to the subspecies which has been called *Anser albifrons gambelli* by previous reviewers of the taxonomy of the species.

ACKNOWLEDGMENT

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BIG TIMBER, MONTANA, 20 MAY 1968.

WINTER DOMINANCE RELATIONSHIP IN BLACK-CAPPED CHICKADEES

JONATHAN E. HARTZLER

DOMINANCE relationships for flocks of birds have been found to vary around two main types. Schelderup-Ebbe recognized individuals within flocks, utilizing marked chickens (*Gallus gallus*), and discovered they were organized into a "peck-right" unilateral despotism, in which the top bird pecks all, the second dominates all but the top one, and so on; the bottom bird pecks none. Similarly, within flocks of pigeons (*Columba livia*) Masure and Allee (1934) described "peck-dominance" organization which was less rigid than in domestic fowl. Individuals of this species pecked one another; however, the dominant birds pecked more and were pecked less than subordinates. Dixon demonstrated peck-right organization within wild flocks of Mountain Chickadees (*Parus gambeli*) (1965) and Carolina Chickadees (*P. carolinensis*) (1963). Due to conflicting descriptions in the literature, the winter flock behavior of Black-capped Chickadees (*P. atricapillus*) is not clear in regard to dominance relationships. Odum (1942) left the status of intermediate members in flocks undetermined, whereas Hamerstrom (1942), also working with Blackcaps, found the dominance order of any two birds was clear, but attempts to arrange the flock as a whole failed. Brewer (1961) concluded that in small flocks of Carolina and Black-capped Chickadees dominance relationships were linear, while in "larger assemblages" deviations from complete linearity occurred. The presence of a dominance hierarchy and the fact that closely related species of the genus *Parus* (Dixon, 1963; 1965) do show winter range defense, suggest that Black-capped Chickadees may also exhibit this behavior. The present paper reports observations of the social organization of Black-capped Chickadees to help clarify their winter dominance relationships.

METHODS

To attract chickadees for trapping, banding, and behavioral observations, continuously baited feeding stations were set in late December, 1967, in a small river bottom woods of approximately 35 acres located 2.5 miles north of Mankato, Minnesota (Fig. 1). The birds were trapped, fitted with a Fish and Wildlife band, and color-marked (Magic Marker on body plumage and Testor's airplane dope on retrices). Observations were carried out over the entire study area; however, the bulk of the data was collected at the five feeders. Criteria for dominance-subordination used in this study were similar to those used by Dixon (1965): (1) successful or unsuccessful attempts at displacement from a perch or food, (2) withdrawal upon detection of an approaching bird, (3) obvious waiting of an individual until another had finished its feeding and departed. Dominance-

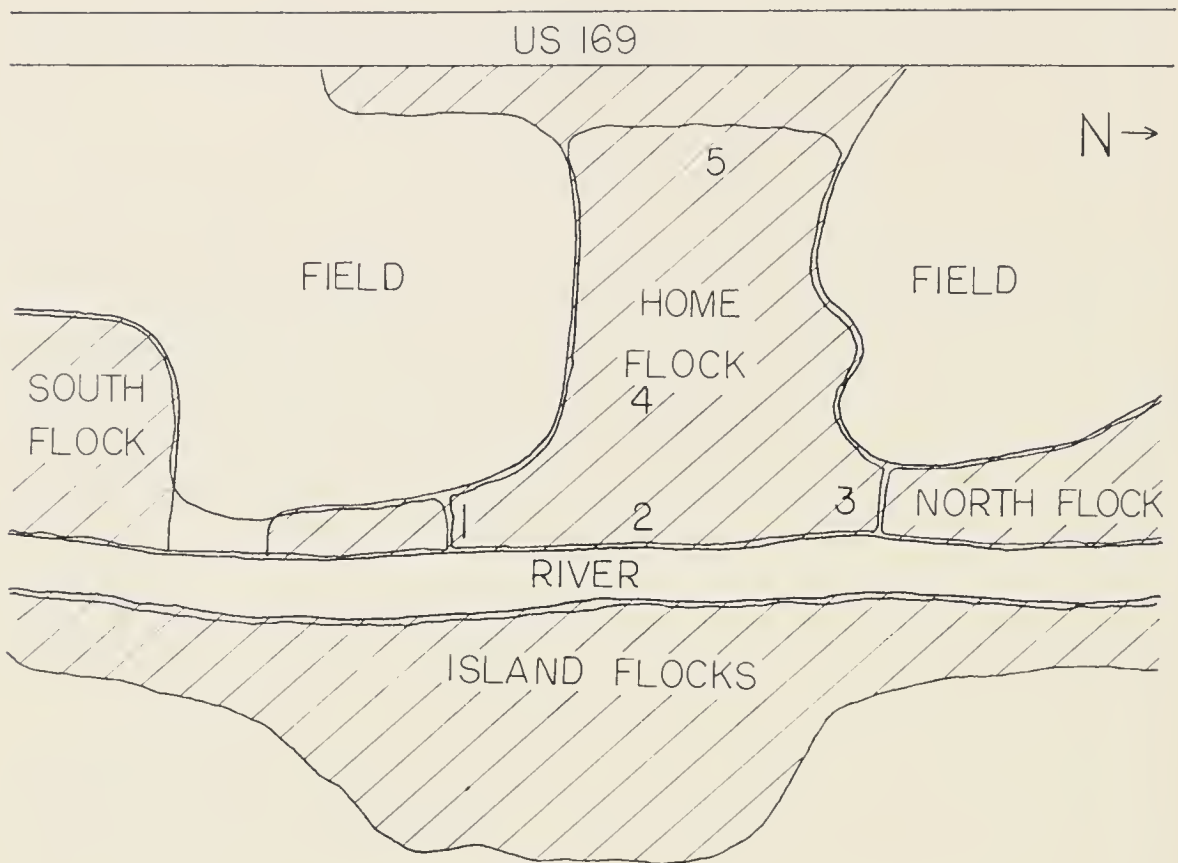


FIG. 1. Map of the study area showing disposition of winter flock ranges, feeding stations 1-5, and association with plowed fields, Minnesota River, highway, and woods (denoted by diagonal lines).

subordination activities were recorded through January and February, 1968. Flock range and composition were ascertained by observations while following the flocks and noting where individuals were seen throughout the study. Attempts were made to arrange individuals within flocks into hierarchies of dominance on the basis of wins and losses at the feeders. If any two individuals next to each other in a hierarchy had no observed dominance encounters with each other, they were arranged randomly with respect to each other, such as BGT and RRR (Table 1). Additional observations were carried out through March and April to ascertain sex and breeding territories.

RESULTS AND DISCUSSION

Flock composition and winter range.—Indications were that the local chickadee population and flock composition varied during the winter. After the initial capture of 20 chickadees from 30 December 1967 to 4 January 1968, no new birds were observed until 29 January when 18 new birds were captured during February. Of the total 38 captured, 7 early captures were members of the home flock; the 18 new captures constituted the south flock, and the remainder were members of the north and island flocks (Fig. 1). The most extensively studied of these flocks, the home flock, occupied a well-defined

winter range of approximately 35 acres. Because of much wandering and trespassing, the winter ranges of the other 3 flocks were not clearly defined. The home flock was almost always in their winter range and generally traveled together, although not all members were always present at any given time. The other flocks, however, were less cohesive and the composition varied so much that much of the time they could not be identified and followed as flocks. Members of other flocks frequently visited the home flock range, especially near the river boundary, and members of the home flock were observed on several occasions to fly across to the island. Odum's (1942) flocks in New York varied in composition, and his average flock range was 35 acres. In Massachusetts, the winter flock range was established in the fall and retained with only minor changes until spring dispersal (Wallace, 1941). In Utah, the Black-capped Chickadee (M. Frydendall, pers. comm.) occupied restricted flock territories of 6 to 8 acres, and the flock composition was stable throughout the winter. It is apparent that flock behavior in Black-capped Chickadees varies. Brewer (1961) emphasized that flock size, as well as degree of constancy of flock composition in chickadees, varies with many factors both of the birds themselves and of the environment.

Intraflock dominance.—Enough gregariousness was present in Black-capped Chickadees so that organized flocking occurred. However, individuals were antagonistic toward each other in that no two birds were ever observed to tolerate each other at close proximity, such as at a 4×8 inch feeder. Intraflock dominance was characterized by a minimum of display, such as posturing, vocalizing, or actual combat; thus, subordinate individuals readily gave up feeders upon approach of a dominant bird and would not challenge dominants at the feeders. During this study a subordinate individual was often observed to withdraw from a feeder when a dominant individual was approaching on the wing at a distance of 10 to 15 yards. In order for such coordination to exist between dominant and subordinate flock-mates, Black-caps must be able to efficiently recognize other individuals. Similar observations were reported by Dixon (1965) in the intraflock dominance contests of Mountain Chickadees.

Within the home flock, individuals were organized into a peck-right dominance hierarchy which held wherever the flock traveled within the flock range. Table 1 summarizes the dominance-subordination data for the members of the home flock. These observations are from five different locations inside the home flock range (feeding stations 1–5, Fig. 1); thus a true peck-right dominance hierarchy existed for this flock of birds because the hierarchy was constant at different locations. Mountain Chickadees (Dixon, 1965) and Carolina Chickadees (Dixon, 1963) also showed a peck-right winter flock organization, but Great Tits (*Parus major*) (Brian, 1949) and Blue Tits

TABLE 1

DOMINANCE-SUBORDINATION RELATIONSHIPS OF THE HOME FLOCK.

Data from all five feeding stations, 2 January to 29 February, 35 days of observation. Winners read horizontally.

	RRR	YTT	GC	BGT	RRF	BRF	RC	Total Wins	% Wins
♂ RRR	—	5	18	8	15	11	7	64	96
YTT	—	—	4	—	9	6	9	28	85
GC	—	—	—	2	2	6	1	11	31
♀ BGT	3	—	—	—	—	3	2	8	44
♂ RRF	—	—	—	—	—	12	6	18	40
BRF	—	—	2	—	1	—	6	9	20
♀ RC	—	—	—	—	—	—	—	0	0

(*P. caeruleus*) (Colquhoun, 1942) both showed social rank in winter flocks dependent on the distance from subsequent breeding territories. Marler (1955) would describe these latter two species as exhibiting peck-dominance because of the effect of location on the dominance outcome. It is necessary that observations from several different locations be used to establish a peck-right hierarchy, because data from a site-dependent, peck-dominant hierarchy, such as in Great Tits, appears to be peck-right if collected from one location only.

Few reversals in the hierarchy occurred during observation (Table 1). On 29 February, the last day the home flock was observed together, the alpha male, RRR, three times allowed BGT to feed while he waited at station 1. However, RRR dominated BGT twice on that day at the same station, and six times prior to this at various stations. Proof of sex was not obtained, but RRR appeared to be a male from his dominance position and role in territory defense in April, 1968, and BGT was his mate (to be further discussed in the spring dispersal section). It appeared that during the winter the male of a pair (RRR) dominated the female (BGT) until near spring dispersal, when he may wait for her to feed. Odum (1942) reports that feeding of the female by the male does not appear in courtship, but occurs later, particularly in incubation. So these reversals of RRR and his mate may be the closest thing to feeding during the early stages of pairing which the Blackcap shows.

Other reversals in the home flock were cases of unexplainable revolts on the part of BRF. Hammerstrom (1942) recorded only one reversal in 76 fights among Blackcaps. However, only actual fights were used as dominance criteria, and the flock as a whole was not arranged into a dominance hierarchy. Odum (1942) called the intermediate birds in his hierarchies "peck-dominant"

because of frequent reversals. The only reversals reported in Carolina or Mountain Chickadees by Dixon (1963, 1965) were the temporary loss of status by mates of alpha males when the males were removed. My study did not indicate high status for the mate of the alpha male; she ranked fourth out of seven. No attempt to remove the alpha male was made in this study.

Spring dispersal.—After traveling together as a fairly cohesive unit during January and February, 1968, the home flock was observed broken up into pairs on 6 March and subsequently never seen again as a unit. Four members of the home flock, RRR, BGT, RRF, and RC, were observed as pairs in the east half of the home flock woods. RRF and RC, fifth and last in the home flock hierarchy respectively, occupied the middle portion of the home flock range next to the river and were observed as a pair 15 March, 2 April, and 21 April. When seen together RRF appeared to be the male from his singing and general aggressiveness. Dixon found alpha males, but no individuals low in the hierarchies, of most winter flocks remained to establish pair territories within the flock range in Carolina Chickadees (1963) and Mountain Chickadees (1965). RRR and BGT, first and fourth in the home flock hierarchy respectively, occupied the central portion of the home flock woods and were observed together 6 March and 21 April. On 21 April, while their mates fed nearby in the home flock woods, RRR actively directed the “*phoebe*” territorial song of the Blackcap at RRF, who actively replied. This singing duel lasted for nearly 30 minutes, and is further evidence that RRR and RRF were males and RC and BGT females. Of the other home flock members only YTT, second in the hierarchy, was subsequently observed after dispersal, on 6 March and 15 March, foraging in the strip of trees beside the highway, approximately 300 yards from the home flock winter range.

Interflock dominance.—Dominance between flocks of Black-capped Chickadees was less well defined than that within the home flock. Members of the home flock did not challenge trespassing birds on the border of the home flock range, except RRR and RRF, both thought to be males who were known to have remained in the winter range and established territories. These two males actively challenged two dominant birds from the south flock. Late in February, RRR and RRF went through extensive posturing, calling, chasing, and actual physical combat with two intruders on the border between the home flock and south flock winter ranges at feeder 1 (Fig. 1). In these encounters RRR and RRF of the home flock were dominant in all instances except one, when, after a long display and chase, RRR was displaced by a dominant individual of the south flock. These interflock displays were much more violent than the few timid challenges within the home flock. The other members of the home flock were dominant over intruders at the feeders (Table 2) but did not actively challenge or chase any of them. Similar

TABLE 2

INTERFLOCK DOMINANCE-SUBORDINATION ENCOUNTERS OF THE HOME FLOCK.

Data from all intruders over the entire home flock range from 2 January to 29 February, 35 days of observation.

	Wins	Losses	Total	Per cent Won
♂ RRR	28	1	29	97
YTT	22	0	22	100
GC	15	1	16	94
♀ BGT	1	2	3	33
♂ RRF	25	1	26	96
BRF	9	4	13	69
♀ RC	20	5	25	80
Total	120	14	134	90

relationships were found between intraflock and interflock encounters in Mountain Chickadees (Dixon, 1965). One important difference does exist, however: in the Mountain Chickadee the alpha males directed hostilities against all intruders, while in this study the Blackcap alpha male actively challenged only dominant intruders, even though he dominated all at the feeders. An even better perceptual system than in intraflock dominance is indicated here, for all home flock members recognized intruders and RRR and RRF recognized the dominant individuals of the south flock.

The birds of the south flock singled out for attack by RRR and RRF were ALLG and WTBS, who won 75 and 100 per cent, respectively, of their dominance encounters with flock mates. This evidence strongly suggests that ALLG and WTBS were dominant members of the south flock (compare with percentage won of RRR and YTT of the home flock, Table 1). Because of the south flock's late appearance and my difficulty in establishing feeding stations in the south flock woods, sufficient data to arrange the entire flock into a hierarchy are lacking. I suspect that ALLG and WTBS were males and that they established or intended to establish pair territories in the general area of feeder 1, but attempts to locate these and to ascertain their sex failed. WTBS was seen after spring dispersal near station 1 on 6 March 1968.

Because active conflict and interflock dominance appeared to be related to the location of the subsequent breeding territories of the home flock males, Blackcap interflock behavior fits the concept of peck-dominance as modified by Allee (1942) to include the location of the contests. Therefore, Black-capped Chickadees had a system of peck-dominance organization working between flocks, simultaneously with a peck-right system within the flock, similar to the Mountain Chickadee (Dixon, 1965).

With the exception of BGT, the individuals who remained in the winter flock range to establish breeding territories (RRR, RRF, RC) had unusually high numbers of interflock encounters. The males of this group also won more interflock encounters than any other home flock members. Members of the home flock were in general dominant over trespassing birds, winning 90 per cent of all interflock contests observed within the home flock range. Thus all the members of the home flock, whether high or low in the hierarchy, whether or not they established later pair territories within the home flock range, had the advantage of precedence to food over intruders within the home flock range.

The dominance position of an individual within the home flock had an important relationship to its success in interflock contests (Table 2). The alpha male, RRR, had and won more interflock contests than any other bird, while the bottom two birds, RC and BRF, lost more contests than any other birds. However, they still won most encounters at the feeders. The per cent won column of Table 2 shows a trend of decrease down the hierarchy; the average of the top three individuals is 97 per cent while the average of the bottom three is 82 per cent.

Because only RRR and RRF, and not the flock as a whole, actively excluded trespassers from the flock boundary, the concept of a "winter flock territory" does not apply to this species. Odum (1942) uses winter flock range instead, and Dixon (1963) found that Carolina Chickadees did not exhibit group territories, because only the alpha male defended the area against males of other flocks. Thus a "group territory" existed only for the dominant males who remained to nest in the winter range. The remainder joined the dominant males to form the winter flock, but played no noticeable part in winter range defense.

SUMMARY

The winter flock behavior of Black-capped Chickadees was studied in relationship to their dominance hierarchy. Within the home flock a peck-right dominance hierarchy was described, but between flocks dominance relationships were better characterized as peck-dominant. The intolerance of the home flock males to dominant members of other flocks was associated with the location of subsequent breeding territories within the winter range, while the intraflock dominance hierarchy held wherever the flock traveled. Dominance-subordination within the home flock involved little calling, posturing, and no chasing, while interflock encounters did when they involved dominant males.

Observations suggested that individual variability is important in interpreting the behavior of this species. One flock of seven chickadees, the home flock, moved around its winter range with little internal conflict; trespass of subordinate members of neighboring flocks was common, but the visiting birds were subordinate to the residents at the feeders. Dominant individuals of other flocks did not trespass deep into the home flock winter range, but remained on the periphery where they were challenged by dominant

home flock males. The surrounding flocks varied in size from 4 to 18 individuals, were less cohesive, and could not be located at any specified time as could the home flock.

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A COMPARATIVE STUDY OF NESTING FORSTER'S AND BLACK TERNS

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FORSTER'S Terns (*Sterna forsteri*) and Black Terns (*Chlidonias niger*) breed sympatrically in marshes throughout the prairie pothole region of southern Canada and the northern United States (Amer. Ornithol. Union, 1957). Nest-sites of Black Terns typically are on low and wet substrates, but Forster's Terns use higher and drier sites over water (Weller and Spatcher, 1965). This paper reports an effort to appraise potential competition for nest-sites by determining (1) the precise differences in nest-site utilization, and (2) the habitat characteristics of the nest locale which may influence site selection.

Preliminary observations were made during the summers of 1959 through 1963 in connection with studies of other marsh birds. Detailed investigations were conducted during 1966 to 1968 under sponsorship of the National Science Foundation Undergraduate Research Participation Program at Iowa State University. We are indebted to the following students who assisted in field work: James E. Doidge, Leigh H. Fredrickson, Daniel M. Herrig, and Larry O. Zach.

STUDY AREAS AND METHODS

The two major study areas were Rush Lake, south of Ayrshire, Palo Alto County, Iowa, and Dan Green Slough in Clay County, northwest of Ruthven, Iowa. Additional observations were made at Barringer Slough, Smith's Slough, and the Oppedahl area near Ruthven.

Cover maps were prepared annually from measurements made on the ice during the winter and spring, using an aerial photo as a base-map. According to the classification scheme used by Weller and Spatcher (1965) for semi-permanent, fresh-water marshes, Rush Lake was in the "hemi-marsh stage" throughout the study, having nearly equal amounts of open water and cattail (*Typha augustifolia*) and its hybrids. Muskrats were abundant and were responsible for many openings in the emergent vegetation. There was a slight increase in open water from 1966 to 1968. Dan Green Slough was in the "open-water stage" with only a few clumps of cattail as the result of an "eat-out" by a rising muskrat population that used most of the available vegetation for food and lodges. Clumps of cattail became progressively reduced throughout the study. During 1966 and especially 1967, there were few muskrats or muskrat lodges at Dan Green Slough. By 1968, the slough was nearly dry and observations were made only from shore.

Nests were found by using a canoe. Each nest was numbered and marked with a willow pole. The following data were recorded at each nest: (1) clutch size, (2) height of nest bowl above water, (3) origin of the nest substrate, (4) composition of nest

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TABLE 1
FREQUENCY OF OCCURRENCE OF NESTS ON SINGLE SUBSTRATES, 1966-68.

	No. of Nests per Substrate					No. of Nests	Mean ± S.E.
	1	2	3	4	5		
Forster's Tern	73 (86%)	9 (11%)	0	1 (1%)	2 (2%)	85	1.2 ± 0.10
Black Tern	197 (100%)	0	0	0	0	197	1.0 ± —

substrate, (5) diameter of nest substrate at water level, and (6) species and relative abundance of plants that make up the surrounding vegetation at each nest site. Locations of nests were mapped on cover maps.

NESTS AND NEST-SITES

Both species of terns sometimes construct a shallow cup-nest with pieces of emergent plants on a substrate of submergent plants or on floating boards. More commonly, however, they use a substrate where little nest construction is necessary but add a few pieces of vegetation to the rim of a natural depression.

Spacing of nests.—Terns are social birds and usually nest in colonies. Spacing of nests seems to be influenced by the distribution of suitable nest substrates and, presumably, by territorial behavior. We did not study inter-specific behavior, however, and observed no conspicuous interactions.

Nests of Black Terns tended to be grouped in certain favorable areas of the marsh, but their nests were dispersed within these areas. In no case was more than one Black Tern nest found on one substrate such as a muskrat lodge (Table 1). Forster's Terns were more social, however, and nests commonly were grouped in "islands" of cattail. Two or more nests occurred on one lodge 14 per cent of the time (Table 1) and large lodges contained up to 5 nests.

Although we did not study tern nests in small marshes, we did note an absence of Forster's Terns in such places. Small water areas were used by Black Terns but usually these held only one pair, whereas larger marshes held many pairs (Provost, 1947:500).

Substrate utilization.—During the 3 years of intensive study, most nests were on muskrat lodges or feeding platforms (Table 2), but some floating materials were used. Usually they were rootstalks or rafts of emergent vegetation lodged between standing vegetation. At other lakes, we have observed that both species may build nests on floating boards held in place by emergent vegetation.

A comparison of nest-sites used at the two lakes indicates the significance of availability of substrates to their use (Table 2). Rush Lake, in the hemi-

TABLE 2
NEST SUBSTRATE UTILIZATION.

Substrate	Forster's Tern	Black Tern
A. Rush Lake, 1966-68		
Active Muskrat Lodge	58 (68%)	—
Inactive Muskrat Lodge	26 (30%)	42 (48%)
Muskrat Feeding Platform	—	20 (23%)
Floating Cattail Rootstalks	—	10 (11%)
Dead Floating Emergent Vegetation	2 (2%)	16 (18%)
Total	86 (100%)	88 (100%)
B. Dan Green Slough, 1966-67		
Active Muskrat Lodge	2 (10%)	—
Inactive Muskrat Lodge	3 (14%)	8 (7%)
Muskrat Feeding Platform	—	1 (1%)
Floating Cattail Rootstalks	12 (57%)	94 (86%)
Dead Floating Emergent Vegetation	4 (19%)	6 (6%)
Total	21 (100%)	109 (100%)
C. All Nests, 1966-68		
Active Muskrat Lodge	60 (56%)	—
Inactive Muskrat Lodge	29 (27%)	50 (25%)
Muskrat Feeding Platform	—	21 (11%)
Floating Cattail Rootstalks	12 (11%)	104 (53%)
Dead Floating Emergent Vegetation	6 (6%)	22 (11%)
Total	107 (100%)	197 (100%)

marsh condition, had a large muskrat population that provided abundant lodges and feeding platforms on which both Forster's and Black terns nested. Dan Green Slough, in the "open marsh" condition, had only a small muskrat population, and nest-sites associated with muskrat lodges or feeding platforms were relatively scarce compared with Rush Lake.

Almost all Forster's Terns nesting at Rush Lake used large, high muskrat lodges, 68 per cent of which were active (Table 2). Less than 15 lodges were present at Dan Green Slough. However, floating cattail rootstalks were common, and these were used by 57 per cent of the nesting Forster's Terns. In 1960, Rush Lake had a large central open water area with only one large island of cattail. Most of the nests found were in this island although there were numerous muskrat lodges in excellent stands of cattail toward the shore. Of 28 nests located in 1960, 12 (43 per cent) were on floating rootstalks resulting from high water levels; 18 were on muskrat lodges. This colonial

TABLE 3
HEIGHT OF NEST BOWL ABOVE WATER (CM), 1966-68.

Substrate	Forster's Tern		Black Tern	
	No. of Nests	Mean \pm S.E.	No. of Nests	Mean \pm S.E.
Active Muskrat Lodge	58	29.8 \pm 2.5	—	— —
Inactive Muskrat Lodge	31	15.0 \pm 1.8	51	3.4 \pm 0.4
Muskrat Feeding Platform	—	— —	21	2.8 \pm 0.2
Floating Cattail Rootstalks	12	6.0 \pm 0.4	102	3.6 \pm 0.2
Dead Floating Emergent Vegetation	6	4.7 \pm 1.2	23	2.3 \pm 0.3
Total	107	21.4 \pm 5.3	197	3.3 \pm 0.2

behavior reflects another aspect of nesting not well recorded in this study: their sociality seemingly exceeded preference for any specific nest-site.

Similar use of available sites was obvious for Black Terns. Seventy per cent of the nests were associated with muskrat structures at Rush Lake, but none were actively being used by muskrats. Most were old and soggy. Evidently because there were no muskrat lodges, eighty-six per cent of the nests at Dan Green Slough were built on floating cattail rootstalks.

Substrate size.—A gross comparison of height of the nest bowl above water and substrate diameter of Forster's and Black Terns (Tables 3 and 4) indicates that Forster's Terns used larger nest substrates than did Black Terns. Heights of substrates for Forster's Tern nests averaged 21.4 cm (107 nests) above the water compared with 3.3 cm (197 nests) for Black Tern nests. Forster's Terns used nest substrates averaging 138.8 cm (94 nests) in diameter compared with 52.2 cm (197 nests) for Black Tern nest substrates.

TABLE 4
DIAMETER OF NEST SUBSTRATE (CM), 1966-68.

Substrate	Forster's Tern		Black Tern	
	No. of Nests	Mean \pm S.E.	No. of Nests	Mean \pm S.E.
Active Muskrat Lodge	54	171.8 \pm 6.0	—	— —
Inactive Muskrat Lodge	31	104.1 \pm 2.3	52	84.7 \pm 5.8
Muskrat Feeding Platform	—	— —	20	47.9 \pm 6.8
Floating Cattail Rootstalks	4	36.5 \pm 3.5	105	41.6 \pm 1.4
Dead Floating Emergent Vegetation	5	79.9 \pm 2.1	20	27.8 \pm 4.3
Total	94	138.8 \pm 6.3	197	52.2 \pm 2.5

Differences in site selection can be seen by comparing each nest substrate category between the Forster's and Black Tern (Table 3). In 1966, when both species used floating cattail rootstalks on Dan Green Slough, nest bowls of Forster's Terns still averaged 6.0 cm (12 nests) above the water but Black Tern nests averaged only 3.6 cm (48 nests). On inactive muskrat lodges, the average nest bowl height of Forster's Terns was 15.0 cm (31 nests), but those of Black Terns averaged 3.4 cm (51 nests) during 1966-1968.

The use of active muskrat lodges by Forster's Terns when Black Terns did not use this substrate probably does not account for all the difference in nest substrate size between the two species (Table 4). Because deserted lodges tend to flatten out from lack of care, these structures often enlarge during deterioration. Hence, one may conclude that Black Terns actually select smaller substrates than do Forster's Terns and that their use of any wet structure allows greater flexibility in selection of nest-sites.

VEGETATION SURROUNDING THE NEST

The presence and nature of vegetation surrounding the nest was recorded at each nest-site. At Rush Lake, all Forster's Tern nests were associated with an open pool of water. Nests usually were on muskrat lodges or on floating rafts of cattail at the edge of an opening created by muskrats. The higher and drier lodges used by Forster's Terns appeared unaffected by wave action, and vegetation surrounding the nest seemed of little importance. These lodges form an "island" habitat which, like the large "islands" of cattail, are preferred by Forster's Terns over other areas. In contrast, Black Tern nests occurred in a variety of vegetative situations from dense stands of cattail to "open water." In the latter case, their nests were protected from wave action by submergent or emergent plants. A total of 38 Black Tern nests (42 per cent) was found at Rush Lake in open water areas created by muskrats; the nest substrate in this situation was either a deteriorated muskrat lodge or a muskrat feeding-platform.

Floating vegetation (mainly *Lemna* spp.) occurred around nest-sites of both species but was more abundant around Black Tern nest-sites that were protected from wave action by emergent vegetation. Floating vegetation around nest-sites in open water was relatively light in density due to dispersion by wind and wave action. During this study, Forster's Tern nests were initiated before floating vegetation became abundant, but Black Tern nests were initiated both before and after the development of abundant floating vegetation.

CHRONOLOGY OF NESTING

During 1966, Forster's Terns began nesting at Dan Green Slough during the last week of May and at Rush Lake during the first week of June (Fig. 1).

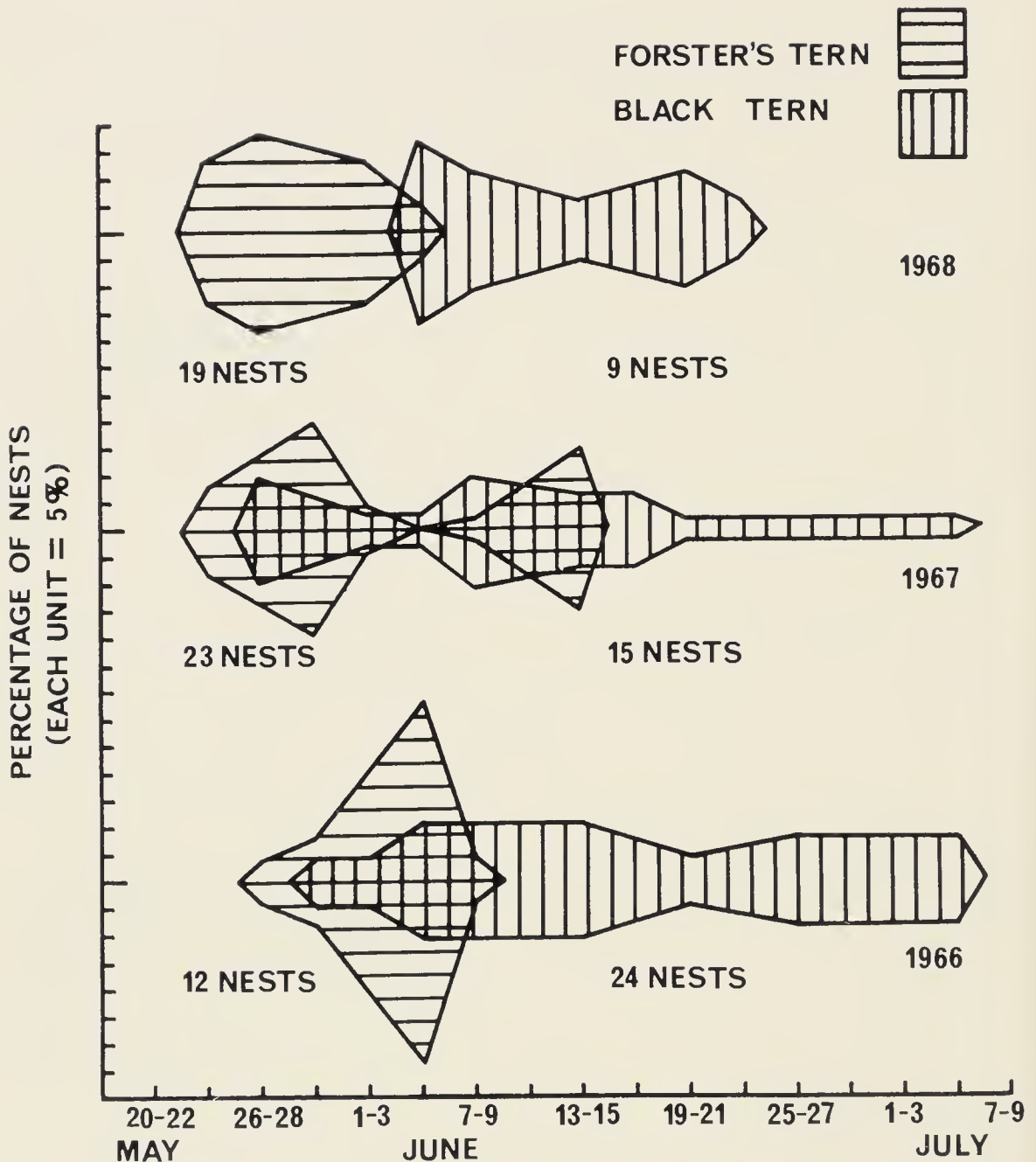


FIG. 1. Chronology of nest initiation by Forster's and Black Terns on Rush Lake (1966-68) and Dan Green Slough (1966-67).

Hatching was complete at both marshes by the last of June. In 1967 and 1968, the first nests of a Forster's Tern colony were found during the last week of May at Rush Lake, but all nests were destroyed within two weeks. In 1967, a second colony began nesting during the middle of June, presumably renesting birds of the first group, but all nests again were destroyed before hatching.

Black Terns began nesting during the last week of May in 1966 and 1967, and new nests were found continually through the first week of July (Fig. 1). In 1967, heavy rains during the middle of June destroyed a large number

TABLE 5
NEST SUCCESS BY NEST SUBSTRATE, 1966-68.

Substrate	Successful	Unsuccessful	Undetermined
Forster's Tern:			
Active Muskrat Lodge	7 (12%)	49 (84%)	2 (4%)
Inactive Muskrat Lodge	3 (10%)	27 (87%)	1 (3%)
Muskrat Feeding Platform	—	—	—
Floating Cattail Rootstalks	1 (8%)	10 (83%)	1 (8%)
Dead Floating Emergent Vegetation	2 (33%)	4 (67%)	—
Total	13 (12%)	90 (84%)	4 (4%)
Black Tern:			
Active Muskrat Lodge	—	—	—
Inactive Muskrat Lodge	18 (39%)	22 (48%)	6 (13%)
Muskrat Feeding Platform	6 (30%)	11 (55%)	3 (15%)
Floating Cattail Rootstalks	24 (23%)	76 (72%)	5 (5%)
Dead Floating Emergent Vegetation	8 (38%)	12 (57%)	1 (5%)
Total	56 (29%)	121 (63%)	15 (8%)

of the Black Tern nests and nests found in early July probably were a product of renesting. In 1968, new nests were initiated from 6 June through 22 June.

Although Forster's Tern nests were initiated only a few days before the first Black Tern nests, the bulk of the colony of Forster's Terns initiated nest simultaneously, but new Black Tern nests were initiated throughout June and into July (Fig. 1).

CLUTCH SIZE

The average clutch size was calculated from the observed clutches only if the egg numbers did not change during one week of observation. Clutch size in both Forster's and Black Terns ranged from 1 to 4 eggs. The average clutch size of 92 Forster's Tern nests was 2.5 (± 0.07) eggs while the average Black Tern clutch was 2.6 (± 0.02) eggs for 151 nests. For both species, clutches of three eggs occurred most frequently (58 per cent of Forster's and 63 per cent of Black Terns), and clutches of 2 eggs were more frequent than clutches of either 1 or 4.

INCUBATION PERIOD

The incubation period was determined by the time elapsed between the last egg laid and the last egg hatched in a clutch. Because nests usually were visited only once weekly, relatively few nests provided accurate records of

incubation periods. Average incubation period for 11 Forster's Tern nests was 24.2 days and for 28 Black Tern nests was 21.4 days.

NEST SUCCESS

Nest success for Forster's and Black terns during 1966 to 1968 is compared by nest substrate in Table 5. Nests were considered successful if at least one young hatched and appeared to have survived at the nest-site. This was determined by rechecking the nest weekly after hatching. The fate of some nests was not determined because evidence of success or failure was not found. Nest success of Forster's Tern nests for which fate was determined was 12 per cent (13 of 107 nests) compared with 29 per cent of 192 Black Tern nests. Causes of failure of tern nests were attributed to one of the following: wind and wave action, muskrat activity, and predation or intraspecific strife. During June of 1967, heavy rains caused rising water levels and increased muskrat building activity. This evidently caused some destruction of Forster's Tern nests because egg shells were found buried under fresh cattail cuttings. Destroyed eggs were found with small punctures so that some intraspecific strife may have been involved (Bongiorno, 1968), but the possibility of damage by other birds cannot be ignored (Pessino, 1968). Wind and wave action evidently caused most of the failures of Black Tern nests during this study, particularly in open areas where the sparse emergent vegetation was not sufficient to protect the low nests.

Unfortunately, there is no obvious pattern of nest success according to nest-site or area. Year by year analyses showed that the best success of Forster's Terns was in 1966 when 36 per cent of 46 nests hatched compared with only 4 per cent of 26 nests in 1967 when heavy rains and rising water levels were involved. There also was a suggestion of higher nest success of Forster's Terns on active lodges (39 per cent of 18 nests in 1966) versus inactive (17 per cent of 12 nests in 1966) or floating cattail rootstalks (8 per cent of 12 nests in 1966).

DISCUSSION

The results of this study indicate that when Forster's Terns and Black Terns inhabit the same marsh, they seemingly do not compete for nest-sites. The most clear-cut difference was the use of higher and drier nest-sites by Forster's Terns while Black Terns utilized lower and wetter sites. Active or recently active muskrat lodges were the only nest substrates utilized by the Forster's Tern at Rush Lake even though other nest substrates were available. Muskrat lodges provide the highest nest substrate on the marsh and seemed to be preferred, but lower sites were used at Dan Green Slough when muskrat lodges or new, high muskrat lodges were not available. Nevertheless, even these

nest sites were larger and higher above the water than were Black Tern nest-sites of similar material in the same marsh. Black Terns nested on a variety of nest substrates at Rush Lake but all were low and wet whereas sites used by Forster's Terns were usually dry.

Black Terns apparently preferred emergent vegetation surrounding the nest-site. The density of the vegetation varied, but this habitat requirement functioned to reduce wind and wave action around the low nest-site. At Rush Lake, Forster's Tern nest-sites were surrounded by open water, which varied from a small pool created by muskrats to a large open pool. Open water surrounding the nest-site may be a result of Forster's Tern utilization of muskrat lodges and not necessarily a nest-site stimulus, but they will use very isolated lodges in the middle of open water. Floating vegetation generally was more abundant around nest-sites of Black Terns because emergent vegetation reduced wind and wave action, but terns nesting late in the season may select for such areas.

Different food habits and methods of feeding also may reduce competition between Forster's and Black Terns. Martin, Zim and Nelson (1951) state that Black Terns are insectivorous, feeding primarily upon mayflies, dragonflies, caddisflies, beetles, and spiders. Forster's Terns eat fish as their staple food although some aquatic insects may be taken. In a publication on gulls and terns of southern U. S. S. R., Borodulina (1966) classified Black Terns mainly as insectivores that occasionally feed on small fish and tadpoles. He observed that Black Terns are especially ichthyophagous in areas where stunned young fish float on the surface. Borodulina also described differences in wing structure and flight behavior that adapts the Black Tern and the black-capped terns of the genus *Sterna* to their common foods.

Possibly the evolution of these terns was one of isolation on small (Black Tern) versus large (Forster's Tern) water areas, which also is related to their insectivorous (Black Tern) versus ichthyophagous (Forster's Tern) food habits. At the present time they nest in the same marshes with little or no obvious competition for nest-sites.

SUMMARY

Forster's Terns and Black Terns occur in the same large marshes, but Black Terns nest in small "potholes" in dense vegetation, or more densely vegetated sites on large marshes. During this study, Black Terns used a variety of low and wet nest substrates, averaging only 3.3 cm above the water. In contrast, Forster's Tern nests were placed an average of 21.4 cm above the water and most frequently were placed on large muskrat lodges (83 per cent). Forster's Tern nests usually were on substrates in or at the edge of open pools of water surrounded by "islands" of cattail but Black Tern nests occurred in vegetative situations ranging from dense stands of cattail to "open water."

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DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, IOWA STATE UNIVERSITY, AMES, IOWA 50010, 12 FEBRUARY 1969.

REQUEST FOR INFORMATION

As a part of the study on Golden Eagle ecology juveniles of this species were color-marked in southwestern Idaho to determine movement and migration patterns. Marked birds carry a crescent-shaped vinyl band around the humeral area of one or both wings. The colors used were red, pink, yellow, orange, dark green, white, and blue. Information desired includes: color of marker on each wing; the date and location of the sighting; and the observer. Send any information to Michael N. Kochert, Idaho Cooperative Wildlife Research Unit, University of Idaho, Moscow, Idaho 83843.

BREEDING BIOLOGY OF AMERICAN COOTS IN IOWA*

LEIGH H. FREDRICKSON

ALTHOUGH the American Coot (*Fulica americana*) has been intensively studied by several investigators, many facets of the breeding biology of the species have not been explored. This paper presents observations on the species in Iowa, made during an experimental study of clutch size in the coot (Fredrickson, 1969).

Sooter (1941) conducted intensive studies on coots in northwestern Iowa. Gullion, who studied a small resident population of coots in California, has made the most detailed observations on the breeding cycle. His publications describe voice differences between the sexes (Gullion, 1950), histology and development of the frontal shield (Gullion, 1951), sex and age determination (Gullion, 1952*a*), molt (Gullion, 1953*a*), territorial and courtship activities (Gullion, 1952*b*), and seasonal variation in interspecific and intraspecific territorial activity (Gullion, 1953*b*). Gullion (1954) summarized his observation on the reproductive cycle of coots in California and compared his findings with information available on other Rallidae. Nest-building, laying, incubation, and hatching were described in detail, but pairing, copulation, and brood-rearing were discussed less thoroughly.

STUDY AREA

The study area was in northwestern Iowa near Ruthven, a marsh area studied and described in detail by Bennett (1938), Low (1945), and Glover (1956). Coots were studied on three marshes, all of glacial origin but modified so that water levels were controllable. The dominant vegetation was cattail (*Typha* sp.), which provided the major nesting cover for coots and other species that nest over water.

METHODS

Nests were located each year by systematically wading or canoeing the marshes. Initiation dates of nests found during laying were calculated by allowing one egg per day. The initiation date was not calculated in nests located during incubation, but embryonic development was appraised by floatation (Westerskov, 1950) or candling (Weller, 1956) as an index to the stage of incubation.

Adult coots were captured for banding and color-marking by using three techniques: nest-trapping, night-lighting, and bait-trapping.

Automatic nest-traps similar to those designed by Weller (1957) generally were successful late in the incubation period; occasionally, however, some birds were captured shortly after laying stopped. Some coots were less broody than others and avoided entering a trap at any time. Thus, the individual broodiness of a coot determined the success of nest-trapping.

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Night-lighting was effective for capturing nesting birds when the study area and nest locations were well known. The technique worked best on dark nights. Coots were most easily caught with a small-sized dip net made of fine "mist" netting. The birds became entangled in the mist netting which allowed fewer to escape. The maneuverability of the light-weight net in the floating vegetation increased the efficiency of capturing coots. If the exact location of the nest and ramp was known before the night-lighting attempt, the incubating coot could be captured as it left the nest.

Gullion's (1950) method of differentiating sex by vocalizations was used. The higher-pitched call of the male is easily distinguished from the lower-pitched notes of the female. With experience, coots also may be sexed by comparing body size, and shape and size of the frontal shield and bill (Gullion, 1951; Fredrickson, 1968).

Adult coots were banded with Fish and Wildlife Service bands and were color-marked in two ways. Each bird was marked with three colored plastic leg bands and a patagial tag, or a nasal saddle, which was visible when the bird was swimming.

The patagial tag was similar to one described by Anderson (1963) but was attached to the patagium by a slightly different method. Either a stainless steel welding rod ($\frac{1}{16}$ -inch diameter) or a stainless steel wire was passed through the patagium and the ends flattened or looped beyond plastic washers to hold the tag in position. The tag was made of a double layer of plastic with colors providing individual identification.

In 1966 nasal saddles (Sugden and Poston, 1968) were used rather than patagial tags. A saddle-shaped piece of plastic was placed over the culmen in the region of the nares. A $\frac{1}{16}$ -inch diameter stainless steel welding rod was passed through the holes bored in the plastic and through the nares of the bird. The ends of the rod were flattened to hold the saddle in place. Color patterns on the tabs identified individuals.

TERRITORIAL BEHAVIOR

Gullion (1952*b*) described territorial behavior and reviewed the literature on aggressiveness in coots. My observations support Gullion's findings. I prefer the term "Chase" over *splattering* but use the terms "Patrol," "Charge" and "Paired Display" as described by Gullion.

I attempted to determine the intensity of the territorial displays and to determine if displays were used in a particular sequence. Intensity was determined by the frequency of display, with displays of lowest intensity occurring most often.

Figure 1 shows the pattern of displays in 30 complete sequences observed in my study. As many as eight displays have been recorded in a sequence. In 27 of the 30 observations, four or fewer displays were involved in each sequence. In 24 sequences, the low intensity Patrol was the initial display. In nine of the 24, the intruder retreated and the contest ended. On some occasions the initial display was of greater intensity than the Patrol. For example, both Charging and Chasing were observed as the initial display. Of 19 sequences with more than one display, eight ended in Paired Display, seven ended in Chase, three ended in Patrol and one ended in Charge.

Coots usually concluded each display sequence with a quick dive regardless of length or intensity of a sequence. On a few occasions the feathers were

FREQUENCY AND POSITION OF DISPLAYS IN A SEQUENCE

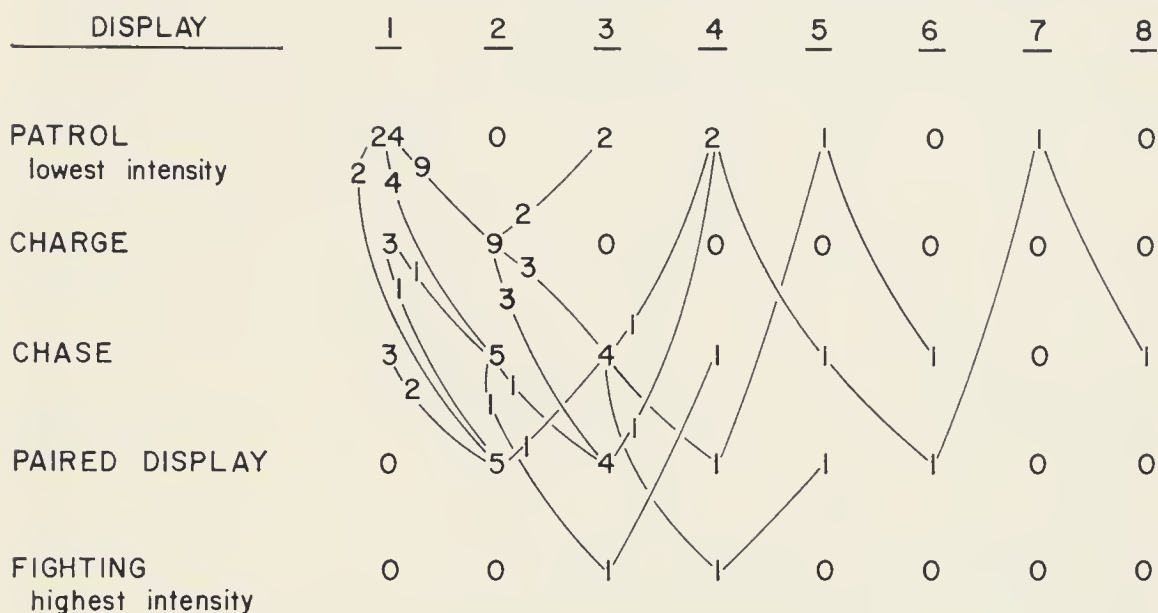


FIG. 1. Frequency of displays observed in territorial activity of the American Coot.

straightened by a Shuffle following the dive. This activity did not occur regularly in the sequence, but occurred commonly during feeding or swimming. Evidently it arranged the feathers over the entire body. The bird moves upward and forward above the water surface. Simultaneously, the wings are elevated slightly above the body. As the head falls forward, the rear portion of the body rises above the water as if the bird were moving over an obstruction. The breast region makes contact with the water first, and the movement ends when the wings return to the normal position.

Several observations of interspecific aggression were made during this study. The degree to which this aggression occurred seemed correlated with the stage of the nesting cycle. Both Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) were driven from the coots' territory in May. Neither Ruddy Ducks (*Oxyura jamaicensis*) nor Redheads (*Aythya americana*) were attacked when encountered late in the nesting season.

REPRODUCTIVE BIOLOGY

Nest and platform construction.—Platform construction is a well-known behavior of nesting coots. Gullion (1954) reported that three pairs constructed as many as nine structures associated with nesting during a single season. Other reports on nest construction were by Wetmore (1920) and Walker (1932) and by Kornowski (1957:341-342) for the European Coot (*F. atra*). In my study, platform building was influenced by the availability of naturally-occurring platforms in the marsh. Coots used muskrat lodges,

TABLE 1

USE OF COVER-TYPE VEGETATION AS NEST MATERIAL BY COOTS IN THE RUTHVEN AREA
IN 1963 THROUGH 1966

Cover-type vegetation	Nest material						Total
	Same as cover-type	Cattail	Cattail and softstem	Cattail and other species	Softstem	All other species	
Cattail	255	255	44	10	8	3	320
Softstem	16	—	—	1	16	—	17
Cattail and softstem	18	—	18	1	8	1	28
Softstem, river bulrush and cattail	—	—	—	—	1	—	1
Cattail and river bulrush	—	—	—	3	1	—	4
River bulrush	3	—	—	—	1	3	3
Hardstem	—	—	—	1	—	—	1
Cattail and sedge	1	1	—	—	—	—	2
Willow	—	1	—	—	—	—	1
Burreed	—	1	—	—	—	—	1
Cattail and hardstem	1	—	—	—	—	—	1
Total	294	258	62	16	35	8	380

feeders, and latrines extensively and built fewer platforms when structures built by muskrats were plentiful.

In my study, nest-building was conducted by both sexes of a marked pair. One bird carried material to the nest site while the mate constructed the nest. The construction and collection activities were often interchanged between the sexes. Although coots used structures built by other species for loafing, copulation, and brooding, all 565 nests in my study were built exclusively by coots.

Coots are very adaptable and will use a variety of materials in nest construction. Possibly dry materials are favored over wet materials, because one pair of marked coots bypassed masses of readily-available floating cattail stalks and traveled to a muskrat lodge to secure dry cattail stalks.

Coots did not appear to favor a particular vegetative type for nest materials. The available material was used regardless of species and whether it was cured or green. Cured material was used most commonly. Cover type and nest material were recorded for 380 nests (Table 1). Of this number, 294 were constructed exclusively of material that existed as cover around the nest.

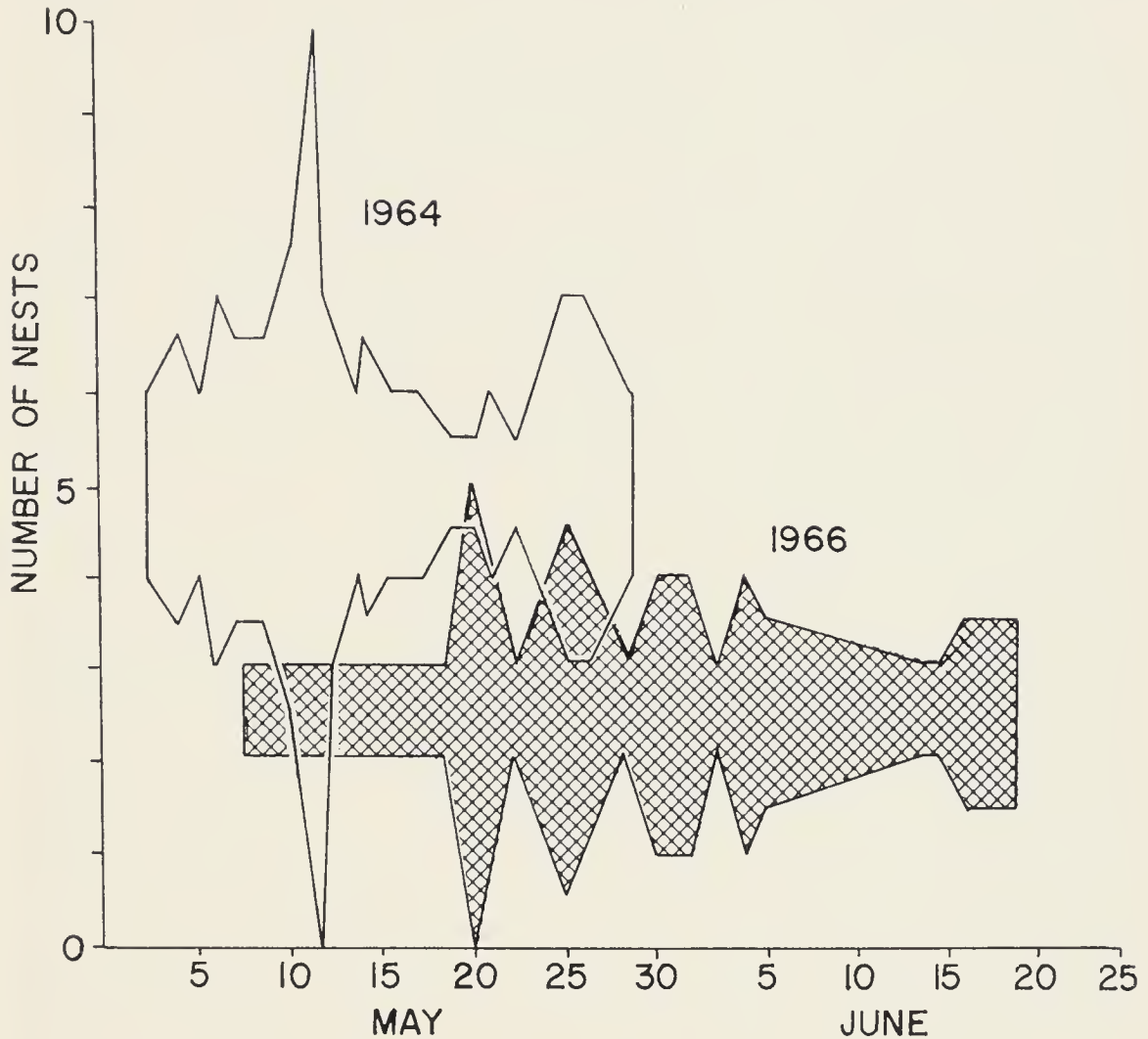


FIG. 2. Chronology of initiation of laying by the American Coot during 1964 and 1966.

Three hundred twenty nests were built in cattail, the most common cover type in these marshes. Of these 320 nests, 255 were built entirely of cattail. Eleven of the nests in cattail were constructed entirely of some other plant species: eight of softstem bulrush (*Scirpus validus*), two of softstem bulrush and arrowhead (*Sagittaria* sp.), and one of river bulrush (*Scirpus fluviatilis*).

Chronology of nesting.—The chronology for initiation of laying was determined in 1964 and 1966 but not in 1965. Dates of initiation were determined either by direct observation or by calculation of the initiation date as described earlier. In 1964, the first nests were recorded on 3 May, with the first peak of initiation of laying occurring on 11 May (Fig. 2). A second peak of initiation occurred 2 weeks later on 25 May. Although coots in California may have two nests each season, no evidence was found that indicated this possibility in Iowa. This second peak may represent reneesting or possibly late nests of young birds.

Nest chronology in 1966 differed from that found in 1964. Unusually cold weather in May probably kept the birds in a nonbreeding condition. The first laying occurred 1 week later than was expected. No well-defined peak of initiation of laying occurred during the season, and nest initiation lasted until mid-June (Fig. 2).

Some coots did not nest until new vegetation was sufficiently high to provide nest materials and a substrate for attaching nests. On two marsh areas near Ruthven, small flocks of coots had territories located in areas with little or no nesting cover until after late May. Coots in one flock began to nest when a dense bed of sweet flag (*Acorus calamus*) had grown to a height suitable for nest attachment. Peak of nesting occurred on this area about 25 June, or 6 weeks later than the first peak (11 May).

Another flock of coots centered their activity in a sparse stand of cattail that was in poor condition due to a muskrat eat-out and flooding. Twenty-five nests were eventually initiated in the area. But the first egg was laid on 18 May, or 15 days after the first eggs were laid in optimal habitat with taller and more dense vegetation. As the cattail developed, more nests were established, and the peak of initiation of laying occurred on 29 May. No nests were initiated later than 21 June. Twenty-three nests with completed clutches of eggs had an average clutch size of 6.3 (range, 3–10 eggs). Of the 25 nests, 9, or 36 per cent, hatched successfully, 7 were destroyed by unknown causes, and 8 were deserted. The fate of 1 nest was not determined.

Copulation.—Observations on copulatory behavior were recorded to determine the seasonal occurrence and the sequence of displays normally involved in this activity. My observations agree with Gullion's (1954:373). Copulatory activity extended over about 1 month, but probably occupied a shorter period of the cycle of each pair. All records of copulation occurred between 13 May and 2 June. Some nests were initiated in early May so copulation must have occurred earlier for some. The period of copulation was closely associated with the egg-laying period. Once a female completed her clutch, copulation was rarely seen. Copulatory attempts, by males, were observed as late as 19 June. Similar findings were reported by Lelek (1958) for the European Coot.

Laying.—The normal pattern of laying has been described by Sooter (1941) and Gullion (1954) who agreed that American Coots lay eggs at intervals of slightly more than 24 hours. Gullion reported a 48-hour gap between two eggs on two occasions, but two eggs were laid on the day following one of these long periods. Sooter (1941) reported that two eggs were laid in two nests in 1 day. These data would be influenced by the recording time and may not reflect the true interval between laying.

Because coots are usually very aggressive, it seemed unlikely that females could avoid the intense territorial defense of most coots to lay eggs in a nest

TABLE 2
DATA ON CLUTCH SIZE OF THE AMERICAN COOT

Clutches				
Number	Range	Mean size	Location	Source and date
169	5-13	9.9	Manitoba	Kiel (1955)
104	1-11	6.08	Iowa	Sooter (1941) for 1936
347	4-18	7.92	Iowa	Sooter (1941) for 1937
15	6-16	8.93	Iowa	Present study 1963
87	6-17	9.85	Iowa	Present study 1964
81	6-13	9.23	Iowa	Present study 1965
98	4-13	8.16	Iowa	Present study 1966
281	4-17	9.03	Iowa	Present study overall mean
8 ^a	7-10	9.0	California	Gullion (1954)
5 ^b	4-8	6.4	California	Gullion (1954)

^a Early season clutches.

^b Late season clutches.

in another territory. It is known, however, that birds of other species do occasionally lay eggs in coot nests. Ruddy Ducks occasionally lay eggs in coot nests (Weller, 1959 and present study). In South America the Black-headed Duck (*Heteronetta atricapilla*) lays eggs in the nests of several species of coots and other birds (Phillips, 1925; Weller, 1968). Promiscuous laying occurs in the European Coot (Alley and Boyd, 1947) and this suggests that similar behavior might occur in the Nearctic form.

Evidence from this study suggests that more than one female might lay eggs in the same nest. Two eggs were added to a nest on 3 consecutive days. The pair associated with nest was marked, and no other coots were observed on or near the nest. Observations on the nest were not continuous, but it seems unlikely that all eggs were deposited by a single female.

Another nest contained 12 eggs; 4 of these eggs were slightly different in shape, were darker in color, and had a different pattern of black flecks than the other 8 eggs. A recent paper by Labisky and Jackson (1966) indicated that caution must be used when associating egg color with a particular female because eggs of the Ring-necked Pheasant (*Phasianus colchicus*) were variable for each hen studied. Because the development of the four eggs lagged a week behind other eggs in the clutch, parasitic laying probably occurred.

In this study, I assumed clutches were the product of two or more females when clutches were in excess of 12 eggs, when eggs were of different sizes or shapes and when two eggs were laid on the same day.

Clutch size.—I examined 565 coot nests. For 281 nests the mean clutch

TABLE 3

FREQUENCY OF OCCURRENCE OF CLUTCH SIZE IN THE AMERICAN COOT IN NORTHWESTERN IOWA IN 1963 THROUGH 1966

Clutch size	Number of nests				Total	%
	1963	1964	1965	1966		
4	0	0	0	3	3	1
5	0	0	0	2	2	1
6	1	3	3	9	16	6
7	4	7	5	22	38	14
8	1	7	15	24	47	17
9	5	17	22	17	61	22
10	2	25	27	14	68	24
11	1	17	3	2	23	11
12	0	6	4	2	12	4
13	0	2	2	3	7	2
14	0	1	0	0	1	—
15	0	1	0	0	1	—
16	1	0	0	0	1	—
17	0	1	0	0	1	—
Total	15	87	81	98	281	—

varied as follows (Table 2): 1963—8.93 (s.d. ± 5.99), 1964—9.85 (s.d. ± 2.16), 1965—9.23 (s.d. ± 1.67), 1966—8.16 (s.d. ± 1.87), and overall mean 9.03 (s.d. ± 2.01). A null hypothesis of no differences between the means was tested with Duncan's new multiple range test (Steel and Torrie, 1960). At the 5 per cent level, the clutch size of 9.85 in 1964 was significantly larger than the clutch size of 8.16 in 1966.

The frequency distribution of clutch size in nests studied from 1963 through 1966 is summarized in Table 3. These data show that clutches with more than 12 eggs or less than 7 eggs were uncommon. Clutches of 10 eggs occurred most commonly, but clutches with 9 eggs were nearly as common. The data presently available on clutch size in the American Coot are inadequate to determine if variations exist in clutch size because of geographical location (Table 2).

Clutch size of the American Coot does vary seasonally. Late clutches in California average 6.4 eggs (Gullion, 1954), or 2.6 fewer eggs per clutch than in early clutches. Much of Sooter's data probably reflect the smaller clutches in late nests. Data collected on clutch size during the 4 years of my study were plotted against time (Fig. 3). Early clutches tended to be larger than late clutches. When the average clutch size was calculated on a weekly basis starting with the first of May, an average of 11.1 eggs per clutch for the

N = NUMBER OF NESTS
 \bar{X} = MEAN CLUTCH SIZE

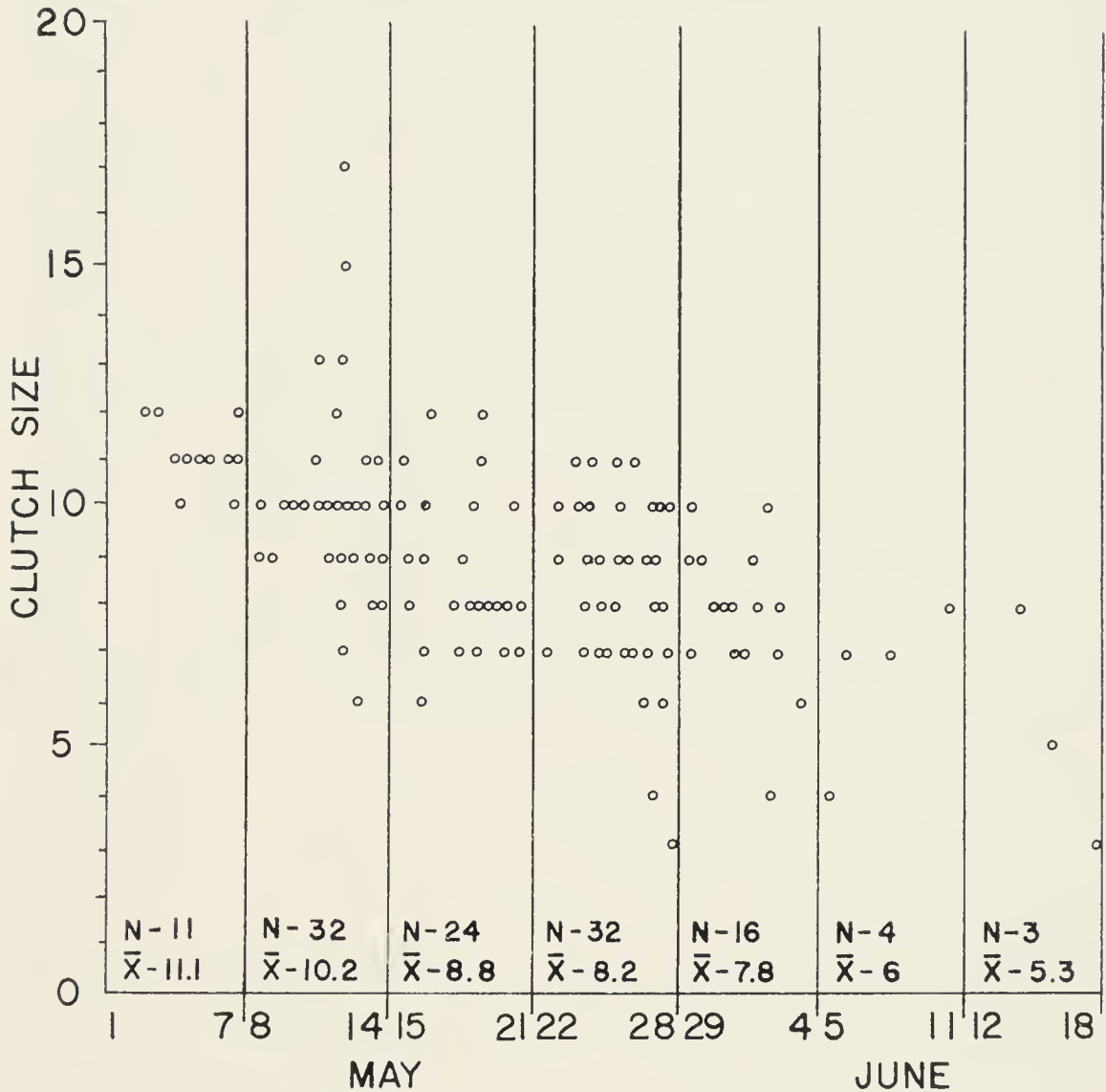


FIG. 3. Clutch size in relation to date of initiation of laying.

first week of May dropped to an average of 5.3 eggs per clutch for the seventh week of nesting. A null hypothesis of no differences between the means for the 7 weeks was tested with Duncan's new multiple range test (Steel and Torrie, 1960). At the 5 per cent level, the following comparisons were significantly different: 11.1 from all means of 8.8 or less, 10.1 from all means of 7.8 or less, 8.8 from all means of 6.5 or less, and 7.8 from all means of 5.3 or less. Similar data have been reported for Blue-winged Teal (Bennett, 1938) and for other dabbling ducks by Sowsls (1955). The smaller clutches appearing later in the season may be the result of renesting or of first nests of young birds.

Incubation behavior.—Researchers studying the American Coot have not agreed on the time of initiation of incubation in relation to the number of eggs in the nest. Sooter (1941) reported that incubation commenced with the first egg, but he did not present supporting evidence. Gullion (1954) observed that incubation began with the first egg only on second clutches. In first clutches, initiation of incubation was variable: some birds started incubation after two eggs were laid, but others completed the clutch before incubating (Gullion, 1954:377). My observations indicated coots spent some time on the nest as soon as the first egg was laid, but evidently incubation was insufficient during the first 3 or 4 days of laying to induce embryonic development. Eggs were generally cold in nests with less than four eggs, but eggs were usually warm in nests with four or more eggs. A similar situation has been recorded for Red-fronted and Red-gartered Coots (*Fulica rufifrons* and *F. armillata*) in Argentina (Weller, 1968:194). Eggs usually hatched over a period of several days, but the appearance of three or four young during the first day of hatching is the result of this incubation behavior.

Because laying and incubation occurred during the same period, some confusion has resulted in determining the length of incubation. Gullion (1954:383) studied this problem closely on four nests by marking eggs as they were laid. The eggs hatched in 23 days. My data are not directly comparable with Gullion's because I used the Heinroth method (interval between the last egg laid and the last egg hatched) to determine the incubation period. Only three nests were checked frequently enough to determine incubation of 23, 24 and 27 days. Four other nests were known to have hatched between 21 and 25 days.

Both members of the pair share in incubation. According to Gullion (1954:378), the male was most often on the nest during the night and for a few short intervals during the day. In 11 observations during my study a nest-changeover ceremony was never recorded, but the possibility of vocal signals cannot be ruled out even though no evidence is presently available to support this possibility.

In eight of the changes observed, one member of the pair had left the nest before the arrival of the mate. In all eight observations the identification of sex was positive. When the incubating bird entered the nest, it preened its breast and belly regions from one to 9 minutes before settling on the eggs.

Brooding.—Because all eggs in the clutch do not hatch simultaneously, coots must continue to incubate but also must feed and brood the young that have hatched. Newly-hatched coots are capable of movement (precocious) and are covered with down (ptilopaedic) and are able to leave the nest as soon as they are dry (nidifugous). Nice (1962) places the rails in her Precocial Category IV, which includes chicks that follow their parents and

are fed by them. Both parents shared in brooding the young, but one of my observations on two marked pairs indicated that the male had a greater share of the brooding responsibility. After all the eggs had hatched young coots traveled with both parents during the day and did not appear to favor one sex. At dusk, when broods moved to platforms, the male seemed to assume the responsibility of caring for most of the young. Observations on two broods with marked adults indicated that in both cases the males brooded five and 10 young respectively and the females remained nearby without young.

Young birds were particularly prone to wetting for a few days following hatching. Feathers of the young birds were oiled directly by billing movements of the adults from their preen glands to the young. Adults also oiled their young by rubbing their oiled underwing and breast feathers on the newly-hatched young. Wild young with parents appeared less prone to wetting than were captive birds that were reared without parental care.

As soon as young coots were dry, they pecked at egg shells and larval insects dropped in the nest. When adults approached, the young birds begged vigorously. The wings were outstretched and moved rapidly in a vertical plane. The head was raised and rotated backward so that the occiput rested against the back or was held directly above it. The head usually moved from side to side.

During the first days following hatching, the young coots appeared dependent on the parents for food. Both sexes collected food for the brood. When one member of the pair was feeding the young at the nest, the mate collected food and then presented it to the incubating bird which in turn fed the young. Larvae of aquatic insects and small crayfish were foods commonly fed to chicks.

Nest sanitation.—Both sexes removed egg shells and vitelline membranes from the nests soon after the young hatched. The adults either ate the egg shells or carried them from the nest and dropped them into the water. Egg shells eaten at the nest accounted for many of the small chips usually associated with successful coot nests.

SUMMARY

Both sexes of the American Coot share in nest construction. Coots used a variety of nest materials but seemed to use materials readily available, particularly dry materials.

The number of platforms constructed by coots during a breeding cycle may depend on the availability of other structures in the marshes such as lodges built by muskrats. Even though coots used other structures for brooding and copulation, coots always constructed their own nests.

Cold spring weather appeared to delay breeding and reduce the average clutch size from 10 to 8. Coots also were influenced by habitat conditions. Birds nesting late in

suboptimal habitat tended to have smaller clutches. It was not known whether this was because of the habitat or merely reflected the physiological condition of birds associated with a particular habitat. In either case, these clutches not only contained fewer eggs but had a lower nest success than birds nesting in good habitat.

Soon after hatching, the parents either ate the egg shells or carried them from the nest and dropped them in water. Because eggs in coot nests hatched over a period of several days, both brooding and incubation behavior were conducted simultaneously. During the first week after hatching, young birds were fed large quantities of aquatic insects and were brooded by the parents. Males appeared to do most of the brooding at night.

ACKNOWLEDGMENTS

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NESTING SUCCESS AND MORTALITY OF NESTLINGS IN A CATTLE EGRET COLONY

JULIAN L. DUSI AND ROSEMARY T. DUSI

THE writers have reported the complete failure, in 1965, of two nesting attempts of Cattle Egrets (*Bubulcus ibis*) in a colony located 15 miles southeast of Dothan, Houston County, Alabama (Dusi and Dusi, 1968). At that time, the slight nesting facilitation effects of a small colony, prolonged drought, and predation, were the ecological factors considered to be responsible for the failures.

During the 1967 season, a strong population and more ideal climatic conditions were present. The season seemed very similar to those of 1963 and 1964, when a strong population was present and a large number of young was produced. The major difference was that in 1963-64, the Little Blue Heron (*Florida caerulea*) was the dominant species and the Cattle Egret a lesser one. In 1967 the Cattle Egret was dominant (about 8,000 adults) and the Little Blue Heron represented by only about 300 adults. Other species were about the same: the White Ibis (*Eudocimus albus*) about 1,000; Common Egret (*Casmerodius albus*) 20; Snowy Egret (*Leucophoyx thula*) 10; and Anhinga (*Anhinga anhinga*) 4 adults.

Because this season very much resembled the previous successful seasons, we felt that an actual measurement of nesting success would be desirable for use in comparison with other seasons.

The nesting started with the Little Blue Herons, Common Egrets, and Snowy Egrets first establishing nests; then the Cattle Egrets came in large numbers to nest and roost, intermingling with the nesting Little Blue Herons and disturbing their nesting with their territorial disputes. This caused a certain amount of destruction of Little Blue Heron nests. Some of the nests were taken over by Cattle Egrets and their eggs deposited with those already laid by the Little Blue Herons.

PROCEDURES

Fifty nests were selected along an erratic transect line. We simply started at one point and took the nests as they came using no selection bias. Tags were placed on the tree trunks about three feet above the water level, where they could be easily seen. A mirror on a pole was used for observing nest contents above eye level. Therefore, the nests were disturbed no more than would be done by walking through the swamp near them. Four trips were made, over a period of 26 days, to evaluate the success of nesting.

RESULTS AND DISCUSSION

In the 50 nests there was a total of 126 eggs, 121 Cattle Egret eggs and five Little Blue Heron eggs, with a minimum of one egg in one nest and a maxi-

num of seven eggs (3 Cattle Egret and 4 Little Blue Heron) in one. Clutch size averaged 2.42 eggs per nest. This is not much more than half of the usual clutch and is perhaps a result of a drought period of some extent before the nesting began. In one of the nests where there were already four Little Blue Heron eggs, three Cattle Egret eggs were added making a clutch of seven; in another there was one Little Blue Heron egg and only two Cattle Egret eggs were added to complete the clutch.

Fifteen nests (30 per cent) were successful and 35 (70 per cent) failed. Of the 126 eggs in the 50 nests, 18 (14.8 per cent) hatched and produced fledglings.

The number of initial failures, 15 (30 per cent) seems quite high. Of these, 14 were nests that were completely gone on the first visit after tagging. Poor construction did not hold them in place or the supporting structure broke and dropped them into the water. At this initial stage of nest development much territorial bickering was still taking place and this additional activity is hard on poorly constructed nests. Whether the birds renested elsewhere in the colony is not known. Nests were established in the colony after this date.

Of the other 21 failures, all but six resulted with the disappearance of the nest. This suggests that poor nest site selection and nest construction are the main causes of nest failure.

The other six failing nests were a result of either desertion, infertile eggs, or possibly predation. The nests either became empty, or nothing happened to the eggs during the study; so, they were either deserted or did not hatch.

In the case of the mixed clutches, eggs became reduced in number to two Cattle Egret eggs in the nest with a total of seven and the nest with two Cattle Egret and one Little Blue Heron eggs was lost. It is of interest, regarding mixed clutches, that in an isolated tree an unnumbered nest contained one young Cattle Egret and one Little Blue Heron, successfully reared together. Therefore, some mixed clutches were apparently reared successfully . . . probably by Cattle Egrets.

One extremely interesting cause of mortality of one of the nestlings was cannibalism (Dusi, 1968). In one nest with two young, examination showed that the three-week-old nestling was trying to swallow its dead 11-day-old nestmate. It had swallowed the head and neck up to the body. The body was too large to be swallowed, resulting in an impasse. We did not alter the situation. The following day, observations showed that the neck of the dead young had parted at the body and the cannibalistic nestmate had apparently finished swallowing the head and neck. We removed the rest of the dead carcass from the nest. It is not known whether the younger bird was eaten alive or whether it had died first. It is known that frequently the younger bird(s) of a clutch

disappear and this observation of cannibalism may provide an explanation to some of this mortality.

CONCLUSIONS

If we consider the nesting success of 30 per cent, insofar as actual nests are concerned (14.8 per cent for the successful transition from eggs to fledged young) and project the probable additional mortality before the young completely leave the nesting colony and then add the 70 to 80 per cent mortality rate for the rest of the first year (Dusi, 1963; Lack, 1949); the questions, not only of, "How can the species survive?", but also, "How can the Cattle Egret be so rapidly increasing in numbers?", are overwhelming apparent.

The picture is depressing and improbable from the individual nesting success standpoint. If, however, we think of the entire colony dynamics . . . the whole population concept . . . then quite a different picture emerges. Early in the nesting season (20 May), we estimated at least 4,000 Cattle Egrets, with 2,000 nests, in the colony. On 10 June, an evening count indicated at least 5,000 adults were present. A one-hour evening count, 4 August, totalled 6,650 adults flying in, in addition to those already in the area. We estimated a grand total of 9,000. Out of this colony we feel that at least 2,000 new individuals have been reared to a size where they were flying from the colony and possibly another thousand was still in the final stages of fledging. Therefore, as a whole, the colony added 2-3,000 new Cattle Egrets to the total population and even though inefficiency had been great, the mass nesting effects have been to greatly increase the numbers of Cattle Egrets.

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ALABAMA, 29 MARCH 1969.

GENERAL NOTES

Mallard-Green-winged Teal associations in southern Wisconsin.—Mallards (*Anas platyrhynchos*) are involved in hybridization more often than any other species of waterfowl (Kortright, *The ducks, geese and swans of North America*, 1967:43). Cockrum (Wilson Bull., 64:142, 1952) records, for North America, only the single wild Mallard \times Green-winged Teal (*Anas carolinensis*) hybrid described by Stone (Auk, 20:209, 1903). Captive hybrids of these species are relatively common (Gray, *Bird hybrids*, 1958:23; Johnsgard, *Condor*, 62:28, 1960). This paper records our observations of two instances of unusual association between a male Green-winged Teal and a pair of Mallards in southern Wisconsin during the summer of 1969.

One trio was first seen on Lake Mendota, Madison, Wisconsin, on 11 April by Nellis. He saw them nearly every day until 19 June when observations were terminated. During these observations, the male Green-winged Teal was always found closely associated with a hen and drake Mallard. The teal was nearly always seen between the male and female Mallards (Fig. 1) and was dominant over the larger drake Mallard. Pre-copulatory behavior was observed several times, but neither drake was ever seen to copulate with the hen. When the drake Mallard attempted to copulate, the teal chased him away, and when the teal attempted to copulate the hen became unreceptive. No aggression was shown by the male Mallard toward the teal. The constant association of these three birds for 70 days clearly suggested that the hen had no nest in this period.

A second Mallard-Green-winged Teal association was observed twice weekly from 2 June until 23 July by Zohrer on a farm pond 40 miles west of Madison. A drake Green-winged Teal was associated with a pair of marked, wing-clipped "wild" Mallards. The



FIG. 1. The usual spatial relationship of the three members of this "trio" with the teal between the Mallards, Lake Mendota, Wisconsin, 13 June 1969.

teal was never seen in association with an additional hen Mallard or a Blue-winged Teal (*Anas discors*) present on this pond. Both in the water and on land the teal was always closer to this particular female Mallard than to any other duck. Aggression was not seen between the three members of this trio.

Several similarities are apparent between these two associations. In both cases, the female Mallard was "paired" with a drake Mallard and a drake Green-winged Teal. Neither hen was observed to copulate with either male. To our knowledge, neither hen produced a brood, and neither was incubating when observations ceased. The potential for hybridization was not realized in either case. Both associations occurred in southern Wisconsin, which is outside the normal breeding range of Green-winged Teal.

We wish to thank P. A. Johnsgard for advice in preparing this manuscript.—CARL H. NELLIS, JAMES J. ZOHRER, AND DANIEL W. ANDERSON, *Department of Wildlife Ecology, University of Wisconsin, Madison, 28 October 1969.*

A second Swallow-tailed Kite record for Trans-Pecos Texas.—On 5 August 1969 an adult Swallow-tailed Kite (*Elanoides forficatus*) was observed soaring over Rio Grande Village, Big Bend National Park, Brewster County, Texas. It remained within a three-mile long area over the Rio Grande or its floodplain, on both sides of the river, including the vicinity of Boquillas, Coahuila, Mexico, from 09:30, when it was first found and photographed by the author, until at least 16:30 when David Easterla observed it there. It remained in flight at all times, gracefully soaring with seven Turkey Vultures (*Cathartes aura*) and two Black Vultures (*Coragyps atratus*).

The record constitutes only the second sighting of the Swallow-tailed Kite for Trans-Pecos Texas. Johnson (Wilson Bull. 80:102–103, 1968) reported a lone bird over Fort Davis, Jeff Davis County (about 120 miles north of Rio Grande Village) on 26 August 1966. However, Pansy Espy (pers. comm.) observed a Swallow-tailed Kite over Fort Davis for 10 days; 25 August to 3 September 1966. These records are undoubtedly of post-nesting wanderers. The species is known to wander widely after nesting; Bent (U.S. Natl. Mus. Bull., 167:52, 1938) reported many fall sightings from New Jersey to North Dakota west to Colorado and Carlsbad, New Mexico. In recent years there have been few fall sightings anywhere but on its regular migration route. In Texas, one was seen north of Fort Worth in Denton County, 22 August 1966 (Williams, Audubon Field Notes, 21:52, 1967); and one was seen near Stockdale, Wilson County, 21 August 1964 (Webster, Audubon Field Notes, 19:57, 1965). Although the species once bred in eastern and central Texas, Wolfe (Checklist of the birds of Texas, 1956:18) considers it to be a "Very rare summer resident in southern area," Galveston to Calhoun Counties, "and rare migrant south to Brownsville."

According to Allan Phillips (pers. comm.), the fact that the bird was seen also over Boquillas, Coahuila, Mexico, constitutes the westernmost Mexican record and only the second for Coahuila. Friedmann, Griscom, and Moore (Distributional checklist of the birds of Mexico, Part I, Pacific Coast Avifauna, No. 29:48) do not include a record for Coahuila.—ROLAND H. WAUER, *Big Bend Natl. Park, Texas 79834, 24 September 1969.*

Giant water bug in an owl pellet.—Great Horned Owls (*Bubo virginianus*) and other owls feed on a variety of animals including even scorpions and centipedes (Bent, U.S. Natl. Mus. Bull., 170:1938). The ability to consume species that possess stinging or biting body parts associated with toxic substances seems remarkable. On 12 October 1969 an owl pellet, probably that of *Bubo virginianus*, was found below a TV tower near Bithlo, Orange County, Florida. The pellet consisted largely of hair from an opossum (*Didelphis*

marsupialis) and a giant water bug (*Lethocercus* sp.) (Hemiptera: Belostomatidae). The insect was intact and about 5 cm in length. Giant water bugs can inflict a notably venomous bite.—WALTER KINGSLEY TAYLOR, *Department of Biological Sciences, Florida Technological University, Orlando, Florida 32816, 20 November 1969.*

Egg transport recorded for the Red-bellied Woodpecker.—The activities of a pair of Red-bellied Woodpeckers (*Centurus carolinus*) at a nest hole seven feet above the ground in a tree and 20 feet from my apartment door in Tampa, Florida, held my attention every morning, in the spring of 1968. On 25 June 1968, at 08:00, I suspected that perhaps one of the parents was feeding young since the tail of one of the woodpeckers bobbed in and out of the nest hole. A moment later it flew directly towards and only a few feet above me and disappeared behind some nearby buildings. As soon as it left the nest I noticed an unbroken, white egg in its bill, presumably its own, oriented with the larger end towards the tip of the bill. Unfortunately, I was unable to determine the sex of this bird.

Egg transport, due to destruction of the nesting tree, has been recorded on film for the Pileated Woodpecker in Florida and noted for the Yellow-shafted Flicker in Massachusetts due to disturbances by Starlings (Truslow, *Living Bird*, 6:227–236, 1967). A record of the Red-bellied Woodpecker transporting House Sparrow eggs is given by Brackbill (*Bird-Banding* 40, 323–4, 1969). A high population of Starlings, one pair of which eventually occupied the evacuated nesting hole, may have been responsible for this unusual behavior in this present sighting.—GRAHAM C. HICKMAN, *Dept. of Biology, Texas Tech University, Lubbock, Texas 79415, 26 January 1970.*

Eastern Phoebe nesting in old Barn Swallow nest.—The Eastern Phoebe (*Sayornis phoebe*) often chooses unusual nesting sites and occasionally uses a nest, with repairs, in successive years (Bent, *U.S. Natl. Mus. Bull.*, 179:141–142, 1942). I have found only one recorded instance, however, of a Phoebe laying in an abandoned nest of another species. Stoner (*New York State Mus. Circular*, 22:1–42, 1939) reported a case where a phoebe lined an old Barn Swallow (*Hirundo rustica*) nest with horsehair and successfully fledged a brood from it. On 8 June 1969, I inspected for possible reuse old Barn Swallow nests in a culvert near the Purdue Golf Course in West Lafayette, Indiana. A phoebe was flushed from a previous year's Barn Swallow nest which had been unused this year. A check of the nest showed that it contained four fresh phoebe eggs. The nest was attached to a vertical concrete wall about five feet above a small stream which flowed through the culvert. It was made completely of mud and straw and apparently had not been modified by the phoebe. The eggs were resting on a few coarse straws which covered the mud base.

Subsequent checks revealed that these eggs were the complete clutch. On 26 June, all of the eggs had hatched and the adult phoebes were feeding the young. On that day, Russell E. Mumford, Purdue University, verified that the nest's construction was that of the Barn Swallow. On 11 July, I flushed two fully fledged phoebes, able to fly well, from the nest, and they landed near an adult in a bush just outside of the culvert.

Earlier in the year, on 4 May, a typical phoebe nest was found under the same culvert with a full clutch of four eggs. It, too, was attached to the vertical wall and was composed primarily of mud and moss. Bent (op. cit.: 142) said that moss is "a constant component of phoebe's nests." The eggs had disappeared on 15 May and I removed the nest. It is possible, although not determined, that it was the same female that built this earlier nest and later used the old Barn Swallow nest. If this was the case, it may be that, being

ready to lay, she returned to reuse her old nest and, finding it gone, occupied the nearby (10 feet) Barn Swallow nest.—HARMON P. WEEKS, JR., *Department of Forestry and Conservation, Purdue University, Lafayette, Indiana 47907, 17 November 1969.*

Hermit Warbler in Missouri.—On the afternoon of 20 December 1969 I observed a Hermit Warbler (*Dendroica occidentalis*) at an eight-acre conifer grove, 10 miles west of Maryville, Nodaway County, Missouri. The warbler was feeding in Scotch pines (*Pinus sylvestris*) and Austrian pines (*Pinus nigra*) with Pine Siskins (*Spinus pinus*) and Golden-crowned Kinglets (*Regulus satrapa*). The warbler was collected and preserved as a study skin (DAE 2290). It was a first year male (skull slightly ossified; testes less than 1 mm; 10.5 gms; moderately fat) that appeared to be in good health.

The Hermit Warbler has not been previously reported from Missouri (Easterla and Anderson, Checklist of Missouri birds. Audubon Soc. of Mo., 1967) and is accidental in the eastern and midwestern United States with only two records (Cambridge, Minnesota [A.O.U. Check-list, 1957:496] and Cambridge, Massachusetts [Audubon Field Notes, 18:425, 1964]) being reported. Besides several records from coastal California, this is the only other United States winter record for *D. occidentalis* (Ibid.). The factors which influenced this bird to stray to Missouri are unknown. That it was healthy and was surviving a Missouri winter seems remarkable since this species normally winters in central southern Mexico (Ibid.). At the time of observation the temperature was 20°F and had been below freezing on previous days. Examination of the proventriculus and gizzard indicated an insectivorous diet which was surprising considering the time of the year. Food items were: stink bugs (Pentatomidae), pigmy locusts (Acrydiinae), ground beetle (Carabidae), leaf beetle (Chrysomelidae), checkered beetle (Cleridae), leafhopper (Cicadellidae), and spider (Arachnida-Araneidae).

Appreciation is extended to Leroy Korschgen and Wilbur Enns, Columbia, Missouri, for identification of food items and to Richard C. Banks, National Museum, for confirming identification of the warbler.—DAVID A. EASTERLA, *Department of Biology, Northwest Missouri State College, Maryville, Missouri 64468, 2 February 1970.*

Yellowthroat caught in common burdock.—On 26 September 1966 on the campus of Garden State Academy near Tranquility, Sussex Co., New Jersey, I found an adult male Yellowthroat (*Geothlypis trichas*) caught on the top of the common burdock (*Arctium minus*). Both feet had become entangled in the burs and the bird had fallen helplessly upside down; the legs were crossed and the tips of the primaries of the right wing were entangled in a lower bur. The three-foot plant was in bloom at the time and the burs were noticeably sticky.

While the Yellowthroat was being released, it made no attempt to bite. Judging from the appearance and activity of the bird, it seemed to have been trapped for only a short time. Since it took some effort to release the bird, it seemed clear that it was hopelessly entangled. Had the bird survived the night, it would likely have died during the following day from predation, starvation, dehydration, or exposure.

In my brief search of the literature I have found reports of a Calliope Hummingbird (*Stellula calliope*) entangled in grass (*Setaria verticillata*) barbs (Tucker, Condor, 57: 119, 1955), a Pearly-eyed Thrasher (*Margarops fuscatus*) trapped by sedge (*Scleria lithosperma*) (Bond, Condor, 62:294–295, 1960), two Herring Gulls (*Larus argentatus*) entangled in hound's-tongue weed (*Cynoglossum officinale*) (Nickell, Auk, 81:555–556, 1964), a Common Tern (*Sterna hirundo*) caught in a prickly lettuce (*Lactuca scariola*) plant (Houston, Blue Jay, 24: 79, 1966), an American Widgeon (*Mareca americana*)

stuck in willow (*Salix* sp.) branches (Sherick, Blue Jay, 24: 143, 1966), and a Red-shouldered Hawk (*Buteo lineatus*) trapped by Spanish moss (*Tillandsia* sp.) (Funderburg, Florida Naturalist, 40:65, 1967). In Saskatchewan, young Turkeys (*Meleagris gallopavo*) are reported to frequently get caught in the sticky sap of gumweed (*Grindelia perennis*) (R. W. Nero, pers. comm.). Arthur P. Cooley of East Pachogue, New York, reported a Pine Siskin (*Spinus pinus*) trapped in common burdock (*Arctium minus*) (O. L. Austin, Jr., pers. comm.). The Cornell Laboratory of Ornithology reported a dead Black-capped Chickadee (*Parus atricapillus*) gripped by the burs of a burdock (*Arctium* sp.) in an attempt to extract seeds (Arehibald, Newsletter to Members, 55:4, 1970). From all indications, the frequency of entanglements in vegetation appears to be fairly common especially in the *Arctium* species.—RICHARD D. BROWN, *Science Dept., P.O. Box 10, Garden State Academy, Tranquility, New Jersey 07879, (Present Address: Dept. of Zoology, Ohio State Univ., Columbus, Ohio 43210) 30 December 1969.*

The double-scratch in the genus *Pooecetes*.—During the summer of 1969, I observed Vesper Sparrows (*Pooecetes gramineus*) double-scratching as they fed in a garden plot near Frederick, Frederick County, Maryland. This behavior was observed infrequently and consisted primarily of a rapid backward kick of both feet. Harrison (Wilson Bull., 79:22–27, 1967) had no evidence of this behavior in this genus—WALTER KINGSLEY TAYLOR, *Department of Biological Sciences, Florida Technological University, Orlando, Florida 32816, 20 November 1969.*

Common Grackle kills Cedar Waxwing in air.—During the first week of August, 1966, I saw a Common Grackle (*Quiscalus quiscula*) kill a flying, immature Cedar Waxwing (*Bombycilla cedrorum*). At Lac des Abatis, 40 miles east of Gracefield, Quebec, Canada, I was observing a flock of Cedar Waxwings feeding some 60 feet above a sandy point that jutted into the lake. Evidently an eddy in the air by a lone white pine was providing insects. A Common Grackle flew into the flock from above, hit one bird a blow, apparently on the nape, and followed its fall to the ground. The bird was dead, its neck broken by the time I reached it from 50 yards away. The grackle flew off at my approach. I examined the waxwing and took it to our fishing camp to skin. Looking back, I saw the grackle return, and search for its kill at the spot of the fall. It walked about the area, hunting thoroughly between the short marsh grasses, and then left. The skull of the waxwing showed no ossification.

According to James Baird (pers. comm.) there are a number of references in the literature to Common Grackles killing or attacking birds the size of House Sparrows. Baird and Smith (Wilson Bull., 77:195, 1965) comment on "the improbability of a grackle successfully pursuing and capturing a healthy small bird." Here, however, is an instance.

I am grateful to Mr. Baird for his interest, and assistance, in this note.—ERMA J. FISK, *17101 S W 284 Street, Homestead, Florida, 31 October 1969.*

First nesting colonies of the Lark Bunting in Missouri.—The Lark Bunting (*Calamospiza melanocorys*) is a Great Plains species that has not been recorded breeding eastward into Missouri. Easterla and Anderson (Checklist of Missouri birds. Audubon Soc. Mo., 1967) consider the species as an accidental transient and summer visitant in the northwestern corner of the state. Two specimens and seven sight records are recorded for Missouri, with all of the sight records of recent occurrence.

On the morning of 5 June 1969 while conducting a Breeding Bird Survey in north-

western Missouri, I discovered a colony of breeding Lark Buntings in a field two miles northwest of Tarkio, Atchison County. A minimum of nine males and three females were observed. The males were often observed in aerial song displays when not perched on a weed stalk or fence. That afternoon, I flushed a female from a partially completed nest. The nest (photographed) was in a dug-out depression in a clump of young (10–12 inch tall) cocklebur (*Xanthium* sp.). It was constructed of last year's dead soybean stalks that were scattered throughout the field. For one hour I observed and followed another pair of Lark Buntings that flew to an adjacent, freshly plowed corn field to feed. During this time the male was observed to court and copulate with the female from eight to ten times.

The gonads of a male and female which were collected (DAE 2263, 2264) indicated breeding (testes-15 × 10 mm; ova-5 × 5 mm and below). They weighed 37.5 and 36.5 g.

The colony was in an 80-acre field that had been cultivated and sown (drilled?) to orchard grass (*Dactylis glomerata*) in spaced 12-inch rows earlier in the spring. At the time of discovery the orchard grass was short (8–12 inch tall) with numerous young (10–12 inch tall) cocklebur plants growing between the rows. Plant cover was about equally distributed between cocklebur and orchard grass. The 80-acre field and surrounding farmland has a rolling terrain and at the time the farmland was either freshly plowed corn fields or tall (3 ft) orchard grass.

On 2 June 1969 J. Fairlie observed a courting pair of Lark Buntings in a field near Lake Contrary, south of St. Joseph, Buchanan County. By 4 June a colony of at least 10 males and two females were established. Male Lark Buntings were often observed in their aerial song displays and copulation between pairs was observed twice. On 4 June Fairlie found a female Lark Bunting impaled on a barb wire fence. Loggerhead Shrikes (*Lanius ludovicianus*) were possibly responsible. On 9 and 11 June Fairlie and F. Lawhon observed a female carrying nesting material. Lawhon and Fairlie continued observing this breeding colony up until 1 July when at least two pair (male and female photographed) were still present with both of the females observed carrying food, presumably to young. These two colonies are 59 air miles apart.

The invasion of breeding Lark Buntings into northwestern Missouri appears to be a recent phenomenon regulated by changes in climate and land use that have influenced other western and southwestern fauna to recently expand their range into Missouri (Brown, Condor, 65:242–243, 1963; Schwartz and Schwartz, The wild mammals of Missouri. Univ. Mo. Press, Columbia, pp. 334–335, 1959; Warner, Wilson Bull., 78:289–300, 1966). At the Atchison County breeding colony there was a considerable amount of bare ground between the orchard grass and cocklebur which could have originally attracted the Lark Buntings to the field, perhaps simulating the short grass prairie conditions preferred by the species to the west. Human disturbances such as plowing, cultivating, and the planting of crops undoubtedly make the habitat more favorable for breeding Lark Buntings and could aid the species in extending its breeding range eastward into Missouri.

These two northwestern Missouri nesting colonies are the first breeding records for Missouri and represent one of the easternmost breeding localities for the species. Apparently the nearest breeding site to Missouri is that recorded by Rice (Bull. Kansas Ornithol. Soc., 16:1–2, 1965) who observed a nesting colony during June–July 1964 in northeastern Kansas (Shawnee County) a distance of 90 and 70 air miles southwestward from the Atchison and Buchanan County sites.

Appreciation is extended to Floyd Lawhon and James Fairlie for making available their field notes.—DAVID A. EASTERLA, *Department of Biology, Northwest Missouri State College, Maryville, Missouri 64468 12 January 1970.*

ORNITHOLOGICAL NEWS

The Fourth Annual Arthur A. Allen Award for distinguished service to ornithology was presented to Alexander Wetmore on 17 October 1970 by the Cornell University Laboratory of Ornithology.

Harry C. Monk, Johnson A. Neff, George M. Sutton, and Gordon Wilson were added this year to the list of 50-year members of the Society.

We have learned of the recent death in an automobile accident of James Fisher, one of the English-speaking world's most well-known ornithologists.

FROM THE AOU

At its annual meeting in Buffalo, New York on 5 October 1970 the AOU elected the following officers:

Robert W. Storer, President	Richard C. Banks, Secretary
S. Charles Kendeigh, First Vice-President	Burt L. Monroe, Jr., Treasurer
Joseph J. Hickey, Second Vice-President	Oliver L. Austin, Jr., Editor

The colorplate in this issue has been subsidized by the generosity of one of our members.

The Eastern Bird Banding Association announces that it will again make an award of \$250 to a student, undergraduate or graduate, who uses bird banding in an ornithological study. The deadline for applications for the award must be received prior to 25 February 1971. Further information can be obtained from, and applications should be submitted to: Mrs. Roger W. Foy, Secretary, Eastern Bird Banding Association, Box 164, Ship Bottom, New Jersey 08008.

The Faculty of Zoology and the Office of International Programs of The Ohio State University announce plans for a study tour to Kenya and Tanzania entitled, "Ecological and Biogeographic Problems in East Africa" to be held in the Spring Quarter of 1971. Up to 15 quarter hours of credit can be earned. Further details can be obtained from Dr. Abbot S. Gaunt, Academic Faculty of Zoology, The Ohio State University, Columbus, Ohio 43210.

The United States National Museum has recently been divided into two separate Museums, the National Museum of Natural History and the National Museum of History and Technology, both bureaus of the Smithsonian Institution.

The U. S. National Museum now consists only of the Office of the Registrar, Administrative and Exhibit Offices.

Because all national biological and paleontological specimens (including those of the

former Biological and Geological Surveys, and Fish and Wildlife Service) have been and still are accessioned through the Office of the Registrar, it is appropriate to continue the designation, USNM, for specimens in all Smithsonian Museums.

During the second half of 1971 the bird collections of the British Museum (Natural History) will be moved from London to the Zoological Museum, Tring, Hertfordshire. The earliest stages of the move will begin about April, and from then until the move is completed it will not be possible for the museum to provide all the usual facilities for visitors or to send out loans from all parts of the collection. For a period of several weeks in the second half of the year it will be necessary to close the collection to visitors.

The collection will be re-housed in what was the Rothschild Museum at Tring, to which a substantial new wing is being added.

LOUIS AGASSIZ FUERTES RESEARCH GRANTS

These grants, established in 1947, are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic organizations. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge.

An anonymous donor gave \$500 to found the fund; later donors have provided additional money. The Council of the Wilson Ornithological Society has added funds as necessary to provide at least one \$100 grant annually. Two grants have been made in several recent years; last year the grants were for \$200 and \$100.

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 *Bulletin* for consideration.

Since its inception, the Fuertes Research Grant has been awarded to 29 persons, many of whom have continued their research work.

Application forms may be obtained from Val Nolan, Jr., Department of Zoology, Indiana University, Bloomington, Indiana 47401. Completed applications must be received by 1 March 1971.

A new award of \$100 annually, to be known as the Margaret Morse Nice Award, has been made possible by the generosity of an anonymous donor of \$500 to the Wilson Ornithological Society. Candidates for this award are limited to persons not affiliated with a college or university. Interested persons should write to Val Nolan, address given above.

ORNITHOLOGICAL LITERATURE

BIRDS OF NORTH AMERICA. By Lorus and Margery Milne. Prentice-Hall, Englewood Cliffs, New Jersey, 1969: 9 × 12 in., 13 + 340 pp., 300 paintings by Marie Nonmast Bohlen. \$25.00.

We have here a bookseller's dream—something big, splashy, and expensive—to capitalize on the ever burgeoning market for books about birds. The publisher tells us on the jacket's front flap that this is "a distinguished portfolio . . . of 300 full-color paintings of birds—breathtaking renditions which have been widely acclaimed by art critics. . . . [The] portraits give details of plumage and markings which are not captured by even the most accurate cameras." Finally, after extensively praising the literary style of the text, the publisher proclaims: "To established bird lovers, this book is indispensable; to novices, it is an irresistible introduction to some of the most beautiful creatures of one continent. . . . *North American Birds* is a valued addition to every home, school, and library."

In no respect can this book be any such addition. As a portfolio of bird art it is nothing less than a travesty. Each species, usually represented by an adult male only, is depicted in exaggerated and often unlife-like colors. Worse still, the publisher has chosen to blow up the paintings to startling size, thereby detailing and accentuating their dismal failure as accurate delineations. Thrushes, mimids, indeed all passerines, as well as plovers and other non-passerines, have the same scutellated tarsi. In flight, some species have anywhere from five primaries (e.g., the Western Bluebird, p. 20) to a dozen (the Pintail, p. 241, has 15 primaries in one wing and 11 in the other). The spread toes of the Semipalmated Plover (p. 306) fail to indicate the reason for the species' name, and the foot of the Belted Kingfisher (p. 291) gives no suggestion of syndactylism. The bill of the American Redstart (p. 119) is typically parulid rather than flycatcher-like as it should be. And so on. While these inaccuracies might be forgiven as artistic license, the inept and frequently ludicrous form of bird after bird cannot. The worst depictions are those of birds in flight. Wings, in some cases no more flyable than an angel's, appear boneless, out of proportion to body, and improperly positioned. Many birds (e.g., the Ruby-crowned Kinglet, p. 111) look stiff, as if in rigor mortis, their feet and toes grotesquely angled and extended.

There are gross errors. The painting of the Gray Jay (p. 193) is labelled Clark's Nutcracker; the painting of the Clark's Nutcracker (p. 101) is labelled Gray Jay. And there are misspelled scientific names (pp. 93 and 299).

What there is of text is brief and, while factually acceptable, contributes little or nothing that cannot already be found in current field guides. Information about each species, usually given on the page with the painting, or on the one opposite, is mainly an elucidation of what the painting shows with additional mention of sexual differences (or similarities) and, if space allows, food habits, habitat preferences, etc. (There is no explanation as to why the male Summer Tanager, p. 127, is shown on the nest.) Occasionally the total information on one species is contained in a single sentence.

So much for my comments on the book. Disturbing as are its many shortcomings, even more disturbing has been its ready and uncritical promotion by parties who should be discriminating in their choice of bird books. A national wildlife organization and one of the largest state Audubon societies, whose officers are surely qualified to judge the value of a bird book, circularized their members with an eye-catching flier extolling this work as indispensable and suggesting its purchase directly from their home offices. Were the officers so gullible as to accept the publisher's claims without first perusing

the work, or were they so zealous for income as to take on a patently sellable item without regard for its value? Only slightly less disturbing have been reviews or notices of this book in some local ornithological and conservation journals that have simply repeated the publisher's claims without any qualification whatsoever. Procedures of this sort reflect deplorable irresponsibility on the part of organizations and journals. To their members and subscribers they are doing a great disservice.—OLIN SEWALL PETTINGILL, JR.

WILDLIFE MANAGEMENT TECHNIQUES. By Robert H. Giles, Jr., editor. The Wildlife Society, 1969: 11¼ × 8¾ in., 623 pp. \$10.00.

The increasing sophistication of technology has provided biologists with an imposing array of electronic and mechanical gadgetry with which to make refined measurements and gather kinds of data previously unobtainable. Most of this technology has been developed for laboratory use; but the techniques utilized by field biologists have also been broadened and refined, although the field biologist more often can implement his research with simpler equipment than can the laboratory technician.

"Wildlife Management Techniques" has undergone a gradual evolution that began in 1938 and has passed through seven editions with several different titles and editors.

The present volume is an attractive publication filled with valuable information on a wide variety of topics pertaining to techniques utilized in wildlife biology. Twenty-five contributing authors wrote 24 chapters and compiled seven appendices in this 623-page volume. Fifty pages cite approximately 1,800 references, and a thorough index contains some 11,000 items. The book is well illustrated with 202 figures plus numerous tables.

The editor describes this edition as ". . . a textbook and manual for well-educated people working with game mammals and birds." The major aim of the book ". . . is to improve the management of the wildlife resource through more rapid development and improved use of techniques." ". . . the objectives are to describe the major approaches to problem solving, suggest ways of implementing these solutions, describe and direct readers to some of the better techniques and tools now known, and indicate gaps in our knowledge."

The following rundown, although succinct, on the kind of information brought together in this publication will clearly indicate its relevance to a variety of ornithological field problems, whether they involve gallinaceous birds or passerines. Several chapters include such practical information as brand names of supplies and equipment, their costs, and addresses from which the information or materials or both can be obtained.

The scope of the book is broad, including chapters that discuss bibliographic tools and reference sources, methods of setting up reference files and a reprint collection, and procedures for preparing a manuscript for publication. One chapter reviews various types of instrumentations that have been used to gather data in a wide variety of mammal and bird studies—many of them with non-game animals.

The book includes a short, but well written, chapter on computers. Different kinds are briefly described and compared. The author discusses how to evaluate whether or not one should use a computer and concisely describes its use. The chapter also provides several examples of computer use in wildlife management. A chapter on radio-location telemetry includes information on the variety of transmitters, methods of attachment to the study animal, receiving systems, and the degree of accuracy in locating the transmitting organism. This chapter might have been expanded to describe the process of telemetry in greater detail and to review more thoroughly some findings resulting from the use of this technique.

The book's longest chapter concerns the sexing and aging of game birds and mammals. The section dealing with birds describes aging and sexing using plumage, gonads, the bursa of Fabricius, copulatory protuberances, penis, color of soft parts, spurs, size and shape of droppings, weights, measurements of various structures, and stage of molt.

Parts of the chapter on habitat analysis and evaluation provide helpful information including methods of assessing the amount or density of covering vegetation, how to determine the type and condition of the soil, how to measure the productivity of various seed crops, and the analysis of vegetation by sampling quadrats and plots and taking transects. Another chapter considers methods of collecting and preserving biological materials, including study skins, tissue samples, whole specimens, blood samples, and plant materials. Quite incongruous and unnecessary, I think, is a section on preserving game trophies and meat.

More and more field studies require the marking of individuals to determine their role in the social system to which they belong. Thus, ornithologists will find useful the section on trapping live birds, where the authors describe the use of several baited walk-in traps, netting, nest traps, and drugs for capturing birds, plus various ways of marking birds that include imping, banding, and dyeing.

Two chapters dealing with animal populations clearly show the necessary orientation of population studies toward statistical analyses. These chapters include an explanation of the statistics of estimating populations, the various methods of sampling, and methods of taking direct animal counts in the field. Survival, recruitment, sex-ratio, age structure, population size and trends, methods of estimating these parameters, and ways of collecting data for studying populations are discussed.

The chapters lack uniformity in the depth of their treatment. Some are sketchy, while others appear to deal rather thoroughly with the subject matter. The editor acknowledges this in the preface. This edition is almost entirely a newly written publication. Two of the chapters were completed three years prior to publication, however; and another was reproduced directly from the 1963 edition.

For years field biologists working with non-game animals have turned to the pages of *The Journal of Wildlife Management* or to one of the editions of this publication to learn techniques that might be applicable to their own studies; for wildlife biologists have pioneered in developing techniques for gathering field data in many areas of study. Therefore, the usefulness of this volume stretches beyond the limits of those working with game mammals and birds. Ornithologists will find a great deal of useful information here, even though the chapters deal more with mammals than birds, and a few of the chapters have no applicability for one working outside the area of wildlife management.—D. A. LANCASTER.

BIRDS OF THE EARLY EXPLORERS IN THE NORTHERN PACIFIC. By Theod Pearce. Published by the author, 1968: 6 × 9 in., 275 pp., 4 bl. and wh. illustrations. \$7.50 (available from Gray's Publishing Company, Ltd., Sidney, British Columbia).

The author has searched the journals of the travelers who penetrated the North Pacific north of a line between Vancouver Island and Kamchatka before 1830 for references to birds. The excerpts he has extracted, which form the bulk of the text, range in significance from nugatory statements of "an abundance of sea fowls" to historically quite important ones, e.g., descriptions of type specimens and species like the Spectacled Cormorant (*Phalacrocorax perspicillatus*), now extinct. Accompanying the excerpts are the

author's attempts at identifying the birds described in terms of recent nomenclature. Many of the descriptions are tantalizing. The sort of person who, upon receiving a phone call from a neighbor describing an unusual bird at the neighbor's backyard feeder, delights in trying to puzzle out which species it might be from the neighbor's unpracticed descriptions will likewise enjoy matching wits with the author on similarly inadequately described birds.

The accounts are arranged primarily by the country of origin of each expedition and then roughly chronologically. Why James Colnett is listed among the Spanish explorers is not explained.

There are four pages of black-and-white photographs, four to a page, of some of the paintings that the artists on Cook's last voyage, William Ellis and John Webber, made of birds of the North Pacific.

The text is marred by frequent misspellings, clumsy sentences, repeated passages, and incorrectly numbered footnotes, all of which could have been put right by a professional editor. The author has gathered together many accounts from references that are rare or not generally available. For this, and for wading through many volumes to extract what little significant information there was on birds, the author will be thanked by researchers on North Pacific history. However, the book's limited scope and careless editing detract from its general usefulness and appeal.—WARREN B. KING.

THE HILL OF SUMMER. By J. A. Baker. Harper and Row, Publishers, 1970: 8½ × 6 in., 159 pp. \$5.00

There are admittedly as many ways of writing about nature as there are eyes to see and ears to hear. Some skim the surface and from the thin top layer create fine word pictures often lacking in life and substance. "The Hill of Summer" is poetry, in which one word picture flows smoothly into the next. "The sparrows' chirping voices are bright nails in the dry grain of the air." The metaphors might seem exaggerated and almost incomprehensible. But slowly the reader becomes accustomed to the style of writing. And then he discovers how the use of words is made into remarkably apt tools expertly wielded in creating accounts of nature that fascinate by their almost uncanny accuracy and precise deductions. Here is nature writing at its most original. And the full flavors of the landscape, the mood of the moment, the behavior and the habits of the wild life, the philosophies of the author, become shared experiences to remember.

The book deals with an English summer and with English birds. There are especially memorable passages on the Nightjar (*Caprimulgus europaeus*), on the Sparrow Hawk (*Accipiter nisus*) and the Kestrel (*Falco tinnunculus*), a great deal of highly revealing and unsentimental interpretations on the predations of hawks and owls, amazingly closely observed in minutest details.

If at the start the reader is left slightly perplexed, the book grows on him, and he closes it at the end with the distinct feeling of having been given a remarkably penetrating and enchanting look at the wonders of nature by a fine observer and naturalist.

"Suddenly he looks up, scanning my dark shape with bland indifference. Under the pale sunset glow that shines beyond the stained-glass sky of the hawthorns, the owl has the face of a saint. A mouse squeaks, a frail bud of sound, deep in the long grass. The owl stops abruptly, wheeling aside, like a white cloth flicked across my eyes. He thumps down, and the grass swirls open beneath his spreading wings. The mouse is dead."—LOUISE DE K. LAWRENCE.

THE AVIFAUNA OF NORTHERN LATIN AMERICA: A Symposium held at the Smithsonian Institution 13-15 April 1966. Edited by Helmut K. Buechner and Jimmie H. Buechner. Smithsonian Institution Press, Washington, D.C. 1970: 8 × 10½ in., 119 pp., 4 figs. (Obtainable from the Superintendent of Documents, U. S. Government Printing Office). \$3.25.

In our preoccupation with the manifold threats to bird habitats and environment in North America it is easy to forget that something over 200 species of birds which nest in the United States migrate through, or winter in, Mexico, Central America, and the Caribbean. Conservation and protection measures north of the Rio Grande will be of little avail to these species if their wintering habitat disappears south of that river. It has been suggested, for example, that the population of Kirtland's Warbler is controlled, not by circumstances in northern Michigan, but by the amount of available wintering territory in the Bahamas. In 1966, at the suggestion of the late William Vogt, the Smithsonian Institution sponsored a symposium addressed to the general problem of the status of the birds of northern Latin America, and we now have at hand the proceedings of that symposium.

Papers were given concerning the birds of Mexico (A. R. Phillips, R. Hernández Corzo), Guatemala (J. A. Ibarra), British Honduras (S. M. Russell), Honduras (B. L. Monroe, Jr.), Nicaragua (T. R. Howell), Panama (E. Eisenmann), Colombia (A. Olivares, F. C. Lehmann), and Venezuela (W. H. Phelps, Jr.). General papers were given by L. R. Holdridge, John W. Aldrich and Chandler S. Robbins, William Vogt, and Marston Bates. At the close of the conference a set of suggestions and resolutions was drawn up.

The recurring theme of all the papers, and the discussion of them, was the rapid destruction of the tropical forest habitats under the increased pressure of population growth. Many tropical species are facing extirpation, and even extinction in a short time if this continues. Indeed, some highly endemic species may already have become extinct. There was general agreement among the participants that the North American migrants were in no great danger from these changes. The only bright spot in the picture was the participation in the symposium of several Latin American biologists, who pointed out that thoughtful people in these countries and their governments are not unaware of the problem. The great difficulties of remedying the situation in face of the pressures for more agricultural land and the need for much education of the local people were stressed.

This volume makes interesting, although gloomy, reading. It is to be regretted that publication of the material comes four years after the symposium. Although there is a brief appendix outlining a few developments to 1969, one cannot help but wonder, in view of the rates of population growth and of deforestation described in the papers, if most of the matter discussed is not already greatly outdated.—GEORGE A. HALL.

RECENT PUBLICATION

Check-list of the Birds of New Mexico. By John P. Hubbard, 1970. 108 pp., 3 maps. New Mexico Ornithological Society (Box 277, Cedar Crest, N.M. 87008), Publ. 3. \$2.50, post-paid.

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INDEX TO VOLUME 82, 1970

This index includes, in addition to the names of genera, species, and authors, references to the following topics: Anatomy, behavior, breeding, clutch size, distribution, ecology, eggs, evolution, food habits, fossils, habitat, hatching, hybridization, incubation, measurements, migration, mortality, molts and plumages, navigation, nesting, nesting success, parasitism, pesticides, physiology, populations, predation, sex ratios, taxonomy, territory, voice, and weights. Also included are references of biological significance to reptiles and mammals. The names of new forms described in this volume are printed in **boldface** type.

- Acanthis flammea*, 284
Accipiter striatus velox, 92
Aegolius acadicus, 374
Aethia cristatella, 289, 291, 292
 pusilla, 289, 290, 291
 pygmaea, 291
Agelaius phoeniceus, 83, 160, 283, 294
Agriocharis anza, 218
 crassipes, 217, 218
 leopoldi, 217, 218
 ocellata, 218
 progenes, 214, 217, 218
Alca torda, 289, 292
Aldrich, John W., and Kenard P. Baer,
 Status and speciation in the Mexican
 Duck (*Anas diazi*), 63-73
Alectoris sp., 282
Alopex lagopus, 134
Amadon, Dean, see Brown, Leslie, and
 ———
Ameiva festiva, 98
Anmodramus savannarum, 376
Ammospiza maritima, 225
 m. macgillivraii, 164
 m. pelonota, 163
 nigrescens, 158, 161, 164
Anas carolinensis, 461
 diazi, 63, 68, 71, 72
 d. diazi, 68, 69
 d. novemexicana, 63, 68, 69
 discors, 333, 334, 447
 platyrhynchos, 11, 63, 68, 71, 72, 95, 323-
 324, 447, 461
 rubripes, 70
 strepera, 96, 387
Anatomy, 219-220; 289-293
Anderson, Daniel W., see Nellis Carl M.
 and ———
Anderson, Daniel W., and Joseph J. Hickey,
 Oological data on egg and breeding
 characteristics of Brown Pelicans,
 14-28
Anhinga anhinga, 458
Anhinga, 458
Anolis limifrons, 98
Anser albifrons, 6, 421
 a. frontalis, 420-426
 a. gambelli, 420-426
Aphelocoma coerulescens, 282
 ultramarina, 282
Aratinga canicularis, 280, 282
Archilochus alexandri, 225
Ardea cinerea, 20
Arenaria interpres, 99
Arremonops conirostris, 284
Asio flammeus, 99, 134
Aythya, 11
Aythya affinis, 387
 americana, 320, 447
Auklet, Crested, 289
 Least, 289
 Parakeet, 289
Austin, Elizabeth S. (Ed.), Frank M.
 Chapman in Florida: His Journals and
 Letters, reviewed, 238
Baker, J. A., The Hill of Summer, re-
 viewed, 472
Baer, Kenard P., see Aldrich, John W.,
 and ———
Bauer, Kurt M., and Urs N. Glutz von
 Blotzheim, Handbuch der Vögel mit-
 teleuropas. Vol. 1, reviewed, 112
Bauer, W., O. van Helversen, M. Hodge,
 and J. Martens, Catalogus Faunae
 Graeciae, reviewed, 314

- Banks, Richard C., Molt and taxonomy of Red-breasted Nuthatches, 201-205; Re-evaluation of two supposed hybrid birds, 331-332
- Bédard, Jean, *Historic naturelle du Gode, Alca torda*, L., dans le Golfe Saint-Laurent, Province de Québec, Canada, reviewed, 314
- Behavior, 29-52, 53-62, 74-78, 96-97, 98-99, 99, 99-100, 100, 101, 120-121, 167-176, 177-183, 184-188, 189-200, 220, 221-222, 222-223, 225, 225-226, 227, 228, 268-278, 279-288, 310-314, 315, 323-324, 324-325, 326-327, 327-328, 330-331, 391-399, 427-434, 446-447, 450, 454, 455, 461-462, 463, 465
- Bergman, Robert D., Peter Swain, and Milton W. Weller, A comparative study of nesting Forster's and Black Terns, 435-444
- Blackbird, Red-winged, 83, 160, 294-303
- Bobwhite, 243, 244, 248, 256, 262, 265
- Bolen, Eric, and John J. Beecham, Notes on the foods of juvenile Black-bellied Tree Ducks, 325-326
- Bombycilla cedrorum*, 81, 283, 375, 465
- Bonasa umbellus*, 310
- Borth, Melvin, see Dunstan, Thomas C., and ———
- Brachyrhamphus brevirostre*, 290, 291
marmoratum, 290, 291
- Branta bernicla*, 6, 383
canadensis, 6, 334
c. parvipes, 422
nigricans, 6, 383
- Brant, 6, 9, 11
Black, 6, 9
- Breeding, 5-13, 14-28, 95, 96, 141-142, 225, 383-390, 445-457
- Brotogeris jugularis*, 282
- Brown, Leslie, and Dean Amadon, Eagles, Hawks and Falcons of the World, reviewed, 230-235
- Brown, Richard D., Yellowthroat caught in common burdock, 464-465
- Bruning, Donald, Conjoined twin Darwin's Rhea, 219-220
- Bubo virginianus*, 374, 462
- Bubulcus ibis*, 458
- Bucephala albeola*, 334
- Buechner, Helmut K., and Jimmie H. Buechner, editors, *The Avifauna of Northern Latin America*, reviewed, 473
- Buechner, Jimmie H., see Buechner, Helmut K., and ———
- Bufflehead, 334
- Bulmer, Walter, First specimens of Chestnut-collared Longspur and Little Gull from Connecticut, 226-227
- Bunting, Indigo, 80, 81
Lark, 376, 465-466
Ortolan, 160
- Buteo jamaicensis*, 96
lineatus, 465
platypterus, 227, 327
regalis, 374
swainsoni, 96
- Butorides virescens*, 282
- Calamospiza melanocorys*, 376, 465
- Calcarius ornatus*, 226
- Calocitta formosa*, 282
- Campephilus imperialis*, 115, 121, 123, 124, 125, 127, 128
magellanicus, 115, 117, 124, 127, 128
melanoleucus, 126
principalis, 115, 117, 121, 122, 123, 124, 125, 127, 128
robustus, 126
- Campochaera sloetii*, 40
- Campylorhynchus brunneicapillus*, 161, 282, 285
- Caprimulgus carolinensis*, 329
- Carduelis carduelis*, 284
- Cardinal, 77, 83-91, 330
- Caribou, 134
- Carpodacus purpureus*, 284
mexicanus, 270, 315
- Casmerodius albus*, 458
- Catbird, 74, 76, 78, 81, 330, 375, 379
- Cathartes aura*, 462
- Centrocerus phasianus*, 217
- Centurus carolinus*, 463
- Cerorhinca monocerata*, 290, 291
- Cephus columba*, 289, 291, 292
grylle, 289, 291
- Chaffinch, 60, 281
- Charadrius pecuarius*, 100
vociferus, 284
- Charmosyna placensis*, 31, 32, 33, 34, 35, 44, 45, 49

- p. placentis*, 39
pulchella, 36, 39, 45
Chen caerulescens, 6
hyperborea, 6
rossii, 5
Chickadee, Black-capped, 53-62, 331, 374, 427-434, 465
Carolina, 331, 427, 431, 433
Mountain, 427, 429, 431, 432
Chlidonias niger, 435
Chloris chloris, 284
Chondestes grammacus, 304, 376
Chordeiles minor, 227, 374
Christman, Gene M., see Orians, Gordon H., and ———
Chuck-will's-widow, 329
Ciccinnurus regius, 42
Ciconia maltha, 334
Circus cyaneus, 98
Citellus armatus, 271
tridecemlineatus, 261
Clark, George A., Jr., Avian bill-wiping, 279-288
Clangula hyemalis, 383
Clench, Mary Heimerdinger, review by, 109-111
Clutch size, 5-13, 15, 95, 253-255, 304-309, 316, 441, 451, 452, 453
Cochran, William W., see Kjos, Charles G., and ———
Coccothraustes coccothraustes, 284
Coccyzus erythrophthalmus, 374
Colaptes auratus, 81, 282, 329
cafer, 374
pitius, 115, 117
Colinus virginianus, 243, 282
Coluber constrictor, 262, 306, 330
c. anthicus, 330
Columba livia, 189, 284, 427
Condce, Ralph W., The winter territories of Tufted Titmice, 177-183
Condor, California, 158
Contopus sordidulus, 374
virens, 81
Coot, American, 445, 457
European, 447
Red-fronted, 454
Red-gartered, 454
Coracina boyeri, 40
caeruleogrisea, 40
Coragyps atratus, 462
Corvus brachyrhynchos, 98, 261
corax, 386
jugilegus, 282
Cowbird, Brown-headed, 74-78, 260, 304-309
Crow, Common, 98-99, 261
Cuckoo, Black-billed, 374
Cyanocitta cristata, 101, 282, 285, 330
stelleri, 282
Cyclorhynchus psittacula, 289, 290, 291, 292
Cygnus olor, 324
Davis, Frederic W., Territorial conflict in the American Woodcock, 327-328
Davis, G. James, Seasonal changes in flocking behavior of Starlings as correlated with gonadal development, 391-399
Demarce, Salome Ross, Nest-building, incubation period, and fledging in the Black-chinned Hummingbird, 225
Dendragapus obscurus, 83
Dendrocopos lignarius, 115, 117, 120
pubescens, 374
Dendrocygna autumnalis, 325
Dendroica auduboni, 315, 355-369
coronata, 355-369
c. auduboni, 367
c. goldmani, 355, 357, 366, 368
c. hooveri, 355, 362, 369
c. memorabilis, 355, 366, 367, 368
c. nigrifrons, 355, 366, 367, 368
discolor, 281, 283
fusca, 81
kirtlandii, 57, 76, 283
occidentalis, 464
pennsylvanica, 81
petechia, 174, 281, 283, 375
Diamond, Jared M., see Terborgh, John, and ———
Dicaeum geelvinkianum, 43
Dicrostonyx groenlandicus, 132, 137, 155
Didelphis marsupialis, 262, 463
Diphylloides magnificus, 41, 47
Distribution, 64-67, 92-95, 102-103, 223-224, 226-227, 329, 366, 421, 422, 462, 464, 465-466
Dixon, Keith L., and Raymond A. Stefauski, An appraisal of the song of the Black-capped Chickadee, 53-62

- Domicella lory*, 39
Donaldson, Graee, see Hays, Helcn, and
———
Dove, Mourning, 96, 284, 374, 377, 378, 380,
381
Rock, 284
Dovekie, 289
Dow, Douglas D., Indexing population
— densities of the Cardinal with tape-
recorded-song, 83–91
Drewien, Rod C., and Larry F. Fredrickson,
High density Mallard nesting on a
South Dakota Island, 95–96
Dryocopus lineatus, 117
l. similis, 92
pileatus, 117, 118, 124
Duek, Black, 70, 71
Black-bellied Tree, 325–326
Black-headed, 451
Mexican, 63–73
Ruddy, 447
Ducula rufigaster, 39
Dumetella carolinensis, 74, 81, 282, 330, 375
Dunstan, Thomas C. and Melvin Borth, Suc-
cessful reconstruction of active Bald
Eagle nest, 326–327
Dusi, Julian L., and Rosemary T. Dusi,
Nesting success and mortality of
nestlings in a Cattle Egret Colony,
458–460
Dusi, Rosemary T., see Dusi, Julian L., and
———
Eagle, Bald, 20, 220, 326–327
Easterla, David A., First nesting colonies
of the Lark Bunting in Missouri, 465–
466; Hermit Warbler in Missouri, 464
Ecology, 29–52, 79–82, 115–120, 158–166,
243–267, 370–382, 466
Edolisoma montanum, 40
Eggs, 14–28, 77–78, 103, 123, 255
Egret, Cattle, 458–460
Common, 458
Snowy, 458
Eider, Steller's, 147
Eisenmann, Eugene, review by, 106–109
Elanoides forficatus, 462
Elaphe obsoleta, 306, 329
Elgas, Bob, Breeding populations of Tule
White-fronted Geese in northwestern
Canada, 420–426
Emberiza hortulana, 160
Empidonax difficilis, 317
minimus, 81, 374
traillii, 282
Enders, Frank, The double-scratch in the
Seaside Sparrow, 225
Endomychura craveri, 290
hypoleuca, 290, 291
Eremophila alpestris, 226
Erolia alpina, 134
melanotos, 134
Erithacus rubecula, 283
Eudocimus albus, 458
Eudynamis scolopacea, 40
Evans, Roger M., Oldsquaws nesting in as-
sociation with Arctic Terns at Church-
ill, Manitoba, 383–390
Evolution, 5–13, 285–286
Falco columbarius, 374
sparverius, 97, 374
Feduceia, J. Alan, The avifauna of the
Sand Draw local fauna (Aftonian) of
Brown County, Nebraska, 332–334
Ficedula hypoleuca, 283
Ficken, Millicent S., see Ickes, Roy A.,
and ———
Finch, House, 270, 274, 276
Fisk, Erma J., Common Grackle kills Cedar
Waxwing in air, 465
Flicker, 81
Chilean, 115
Red-shafted, 374, 379
Yellow-shafted, 329–330, 463
Florida caerulea, 458
Flycatcher, Crested, 81
Fork-tailed, 92
Least, 80, 81, 374
Western, 317
Vermilion, 315–319
Food Habits, 29–52, 97–98, 99, 101, 101–
102, 136–138, 184–188, 206–213, 222–
223, 228, 325–326, 462–463
Fossils, 214–218, 332–334
Fox, Arctic, 134
Gray, 262
Red, 261
Fratercula arctica, 290
corniculata, 289, 290, 291
Fredrickson, Larry F., see Drewien, Rod
C., and ———

- Fredrickson, Leigh H., Breeding biology of
American Coots in Iowa, 445-457
- Fringilla coelebs*, 60, 281, 284
montefringilla, 284
- Fulica americana*, 445
armillata, 454
atra, 447
rufigrons, 454
- Gadwall, 96, 387
- Gallus gallus*, 282, 427
- Gannet, 158
- Geothlypis trichas*, 281, 283, 375, 464
- Gerygone chloronata*, 35, 40, 47
palpebrosa, 40
- Giles, Robert H., editor, Wildlife Management Techniques, reviewed, 470-471
- Glutz von Blotzheim, Urs. N., see Bauer Kurt M., and ———
- Glycichaera fallax*, 34, 42
- Goldeneye, Barrow's, 220
- Goldfinch, 277
American, 375, 379
- Goose, Blue, 6, 9, 11
Canada, 6, 334
Lesser Snow, 6
Ross', 5-13
White-fronted, 6, 9, 420-426
- Gould, John, Birds of Asia, reviewed, 314
- Graekle, Boat-tailed, 472
Common, 465
- Grebe, Horned, 334
- Greenwalt, Crawford H., Bird Song: Acoustics and Physiology, reviewed, 235-237; How Birds Sing, reviewed, 235-237
- Grisez, Ted, A White-throated Sparrow nests in western Pennsylvania, 102-103
- Grosbeak, Black-headed, 94
Rose-breasted, 81, 280
- Ground Squirrel, Uinta, 271
Thirteen-lined, 261
- Grouse, Blue, 83
Ruffed, 206, 310-314
Sage, 217
Sharp-tailed, 221-222
- Gull, Black-headed, 281
Glaucous, 134, 151
Herring, 20, 189-200, 386, 389, 464
Laughing, 222
Little, 226-227
Ring-billed, 189, 196, 222-223
- Cunn, William W. H., review by, 235-237
- Guillemot, Black, 289
Pigeon, 289
- Gymnocorvus tristis*, 41, 47
- Gymnophaps, albertisii*, 39
- Gymnophithys*, 282
- Gymnostinops montezuma*, 94
- Habia gutturalis*, 284
rubica, 284
- Habitat, 115, 130-132, 160, 370-382, 436-439, 466
- Haliaeetus leucocephalus*, 20, 220, 326
- Hall, George A., review by, 473
- Hammer, Donald A., Trumpeter Swan carrying young, 324-325
- Hanson, Hugh, see Taylor, Walter Kingsley and ———
- Hartzler, Jonathan E., Winter dominance relationship in Black-capped Chickadees, 427-434
- Hatching, 289-293, 318
- Haverschmidt, F., Ruddy Turnstones making use of Yellow-crowned Night Herons for food-finding, 99; Barn Owls hunting by daylight in Surinam, 101; Rufous-crowned Tanagers feeding on fruitbowl, 228
- Hawk, Broad-winged, 227, 327
Marsh, 98-99
Pigeon, 374, 379
Red-shouldered, 465
Red-tailed, 96-97
Rough-legged, 374, 379
Sharp-shinned, 57, 92
Sparrow, 97-98, 374, 379
Swainson's, 96-97
- Hays, Helen, Common Terns pirating fish on Great Gull Island, 99-100
- Hays, Helen, and Grace Donaldson, Sand-kicking camouflages young Black Skimmers, 100
- Hein, Dale, Dust-bathing sites selected by Ruffed Grouse, 310-314
- Hellman, Geoffrey, Bankers, Bones, and Beetles, reviewed, 239
- Helmitheros vermivorus*, 228
- Herbert, A. D., Spatial disorientation in birds, 400-419

- Heron, Little Blue, 458, 459
 Yellow-crowned Night, 99
Heteronetta atricapilla, 451
 Hickey, Joseph J., editor, Peregrine Falcon
 Populations, reviewed, 105-106; see
 Anderson, Daniel W., and ———
 Hickman, Graham C., Egg transport re-
 corded for the Red-bellied Woodpecker,
 463
Hippolais icterina, 283
Hirundo rustica, 463
 Hodge, M., see Bauer, W., and ———
 Hoff, C. Clayton, and Marvin L. Riedesel,
 editors, Physiological systems in semi-
 arid environments, reviewed, 237-238
 Holcomb, Larry C., and Gilbert Twiest,
 Growth rates and sex ratios of Red-
 winged Blackbirds, 294-303
 Horak, Gerald L., A comparative study of
 the foods of the Sora and Virginia
 Rail, 206-213
 Hubbard, John P., Geographic variation in
 the *Dendroica coronata* complex, 355-
 369
 Hudson, J. W., review by, 237-238
 Hummingbird, Black-chinned, 225
 Rufous, 285
 Hybridization, 69, 71, 97, 331-332, 461-462
Hylocichla fuscescens, 226, 375
guttata, 103, 226
mininta, 226
mustelina, 81
ustulata, 226, 375
 Ibis, White, 458
 Ickes, Roy A., and Millicent S. Ficklen, An
 investigation of territorial behavior in
 the American Redstart utilizing re-
 corded songs, 167-176
Icterus bullockii, 375
galbula, 94, 184, 283, 375
 Incubation, 225, 441-442, 454
Iridoprocne bicolor, 282
Ipocrantor, 127
 Jackson, Jerome A., Predation of a Black
 Rat Snake on Yellow-shafted Flicker,
 329-330
 Jaeger, Parasitic, 134, 386, 387, 389
 Pomarine, 130-157
 Jay, Blue, 101-102, 330
 Jenkins, Robert E., Food habits of winter-
 ing Sparrow Hawks in Costa Rica,
 97-98
 Jenkinson, Marion Annc, see Mengel,
 Robert M., and ———
 Johnston, David W., High density of birds
 breeding in a modified deciduous
 forest, 79-82
Junco hyemalis, 81, 103, 284
oreganus, 276
 Junco, Oregon, 276
 Slate-colored, 80, 81, 103
 Killdeer, 284
 King, Warren B., review by, 471-472
 Kingbird, Eastern, 374, 379
 Western, 93, 374, 379
 Kinglet, Golden-crowned, 464
 Kish, Frank, see Wollhuter, Bruce R., and
 ———
 Kite, Swallow-tailed, 462
 Kittiwake, Black-legged, 137
 Kjos, Charles G., and William W. Cochran,
 Activity of migrant thrushes as deter-
 mined by radio-telemetry, 225-226
 Klimstra, W. D., see Roseberry, John L.,
 and ———
Lagopus scoticus, 282
Lalage leucomela, 40
Lampropeltis caligaster, 262
 Lancaster, D. A., review by, 470-471
Lanius excubitor, 283
ludovicianus, 283, 375, 466
 Lark, Horned, 226
Larus argentatus, 20, 189, 284, 386, 464
atricilla, 222
delawarensis, 189, 222
hyperboreus, 134
minutus, 227
ridibundus, 281, 282
Laterallus, 333, 334
 Lawrence, Louise de Kiriline, review by,
 341-342, 472
 Leberman, Robert C., review by, 339-341
 Lemming, Collared, 132
 Brown, 130-157
Lemmus trimucronatus, 130-157
Leucophoyx thula, 458
Limothlypis swainsonii, 228
Lonchura cucullata, 283
punctulata, 283
striata, 283

- Longspur, Chestnut-collared, 226-227
Lophorina superba, 41
Loriculus aurantiifrons, 40, 44
 galagulus, 282
 vernalis, 282
Loxia curvirostra, 284
Lunda cirrhata, 291
Luscinia megarhynchos, 283
Machaerirhynchus flaviventer, 31, 41
Macropygia auboinensis, 39
 nigrirostris, 39
Magpie, Black-billed, 374, 379
Maher, William J., The Pomarine Jaeger
 as a Brown Lemming predator in
 northern Alaska, 130-157
Mallard, 11, 63, 68, 69, 71, 72, 95-96, 323-
 324, 447, 461-462
Mareca americana, 464
Margarops fuscatus, 464
Martens, J., see Bauer, W., and ———
Martin, Larry D., and James Tate, Jr., A
 new turkey from the Pliocene of Ne-
 braska, 214-218
Meadowlark, Eastern, 164, 243-267
 Western, 243, 255, 373, 375, 377, 381
Meanley, Brooke, Method of searching for
 food by the Swainson's Warbler, 228
Measurements, 14-28, 69, 77, 118, 223,
 294-300, 334, 360-361, 424
Melanocharis longicauda, 43
 striativentris, 43
 versteri, 43, 46
Meleagris alta, 218
 gallopavo, 218, 465
Melidectes torquatus, 31, 36, 42, 46, 50
Melilestes megarhynchus, 42, 46
Meliphaga orientalis, 50
Meliphaga spp., 31, 33, 34, 35, 36, 37, 43,
 44, 45, 47, 50
Melipotés fumigatus, 42, 50
Melopsittacus undulatus, 282
Melospiza georgiana, 284
 melodia, 60, 246, 284, 285
Mengel, Robert M., and Marion Anne
 Jenkinson, Parasitism by the Brown-
 headed Cowbird on a Brown Thrasher
 and a Catbird, 74-78
Mephitis mephitis, 261
Merops ornatus, 40
Merrell, Theodore R., Jr., A swimming
 Bald Eagle, 220
Michael, Edwin D., Wing flashing in a
 Brown Thrasher and Catbird, 330-331
Microtus californicus, 153
 oeconomus, 133, 137
 ochrogaster, 262
 pennsylvanicus, 261
Migration, 225-226, 323-324
Miley, Theodore R., Males in breeding
 plumage of the races of the *Dendroica*
 coronata complex, watercolor by, facing
 page 355
Milne, Lorus, and Margery Milne, Birds
 of North America, reviewed, 469-470
Milne, Margery, see Milne Lorus, and
 —————
Mimus polyglottos, 282, 330
Mino dumontii, 37, 41, 47
Mockingbird, 330
Molothrus ater, 74, 260, 283, 285, 304
Molts and plumages, 201-204, 298-299,
 320-323
Monroe, Burt L., Jr., A distributional study
 of the birds of Honduras, reviewed,
 106-109
Mortality, 405-407, 415-418, 458-460
Morton, Eugene S., Chuck-will's-widow in
 Connecticut, 329
Mueller, Helmut C., Circle-soaring by
 migrating nighthawks, 227
Murre, 18, 292
 Common, 289
 Thick-billed, 289
Murrelet, Kittlitz's, 292
Muscivora tyrannus, 92
Mustela erminea, 261
 rixosa, 134, 155
Myiarchus crinitus, 81
Myzomela cruentata, 31, 32, 33, 35, 36, 42
 eques, 31, 33, 35, 42
 nigrita, 31, 32, 33, 35, 42, 45, 46
 obscurus, 47
 rosenbergii, 31, 36, 42
Navigation, 189-200, 400-419
Nectarina sericea, 47
Nellis, Carl H., James J. Zohrer, and
 Daniel W. Anderson, Mallard-Green-
 winged Teal associations in southern
 Wisconsin, 461-462

- Nero, Robert W., Sharp-tailed Grouse gives aggressive display to automobiles, 221-222; review by, 336-338
- Nesting, 5-13, 95-96, 102-103, 119, 225, 243-267, 304-305, 315-319, 326, 370-382, 383-390, 435-444, 445-457, 463, 463-464, 465-466
- Nesting success, 255-265, 304-309, 387, 442, 458-460
- Newman, George A., Cowbird parasitism and nesting success of Lark Sparrows in southern Oklahoma, 304-309
- Nighthawk, Common, 227, 374
- Nothoprocta cinerascens*, 282
- Nuthatch, Red-breasted, 201-205
White-breasted, 81, 286
- Nyctanassa violacea*, 99
- Nyctea scandiaca*, 134
- Oedistoma pygmaeum*, 31, 32, 33, 34, 35, 42, 47, 49
- Oldsquaw, 383-390
- Olor buccinator*, 324, 334
- Opopsitta diophthalma*, 40
gulielmi III, 40
- Oporornis formosus*, 228
- Opossum, 262, 463
- Oreornis obscurus*, 31, 32, 33, 34, 35, 42, 47, 50
- Orians, Gordon H., and Gene M. Christman, A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds, reviewed, 336-338
- Oriole, Baltimore, 94, 184-188, 375, 379
Bullock's, 375, 379
- Oriolus szalayi*, 41, 47
- Oropendola, Montezuma, 94
- Otus asio*, 223-224, 330
a. floridanus, 223
a. gilmani, 223
flammeolus, 223-224
scops, 223
spilocephalus, 223
trichopsis, 223
- Ovenbird, 77, 80, 167, 228, 248
- Owl, Barn, 101
Burrowing, 334
Flammulated, 223-224
Great Horned, 95, 98-99, 374, 379
Sand Draw Burrowing, 333
Saw-whet, 374
Screech, 330
Short-eared, 99, 134
Snowy, 134, 151
- Oxyura jamaicensis*, 447
- Pachycare flavogrisea*, 41
- Pachycephala rufiventris*, 41
soror, 41
- Paradisaea apoda*, 31, 42, 47
raggiana, 282
rudolphi, 42
- Parapavo californicus*, 218
- Parasitism, 74-78, 99-100, 260-261, 307-309
- Parkes, Kenneth C., On the validity of some supposed "first state records" from Yucatan, 92-94; review by, 230-235
- Parotia carolae*, 282
- Parus atricapillus*, 53, 59, 60, 282, 331, 374, 427, 465
atricapillus × *P. gambeli*, 331
bicolor, 81, 177
carolinensis, 56, 282, 331, 427
caeruleus, 271, 430
gambeli, 331, 427
inornatus, 60
major, 282, 429
montanus, 331
- Passer domesticus*, 268, 283
- Passerina cyanea*, 81
- Peakall, David B., review by, 105-106
- Pearse, Theed, Birds of the Early Explorers in the North Pacific, reviewed, 471-472
- Pediocetes phasianellus*, 221
- Pelecanus erythrorhynchos*, 15
occidentalis, 14
o. californicus, 16, 17, 18, 21, 22
o. carolineus, 16, 17, 18, 21, 22
o. occidentalis, 16, 22
- Pelican, Brown, 14-28
White, 15
- Peltops montanus*, 31, 41
- Pesticides, 19-21
- Petrochelidon pyrrhonota*, 374
- Pettingill, Eleanor Rice, review by, 238
- Pettingill, Olin Scwall, Jr., review by, 240, 314, 469-470
- Pewee, Western Wood, 374
Wood, 81

- Phasianus colchicus*, 96, 374
Phalarope, Red, 136
Phalaropus fulicarius, 134
Pheasant, Ring-necked, 96, 374
Pheucticus ludovicianus, 80, 81, 280, 284, 285
 m. melanocephalus, 94
Philohela minor, 160, 327
Phloeoceastes guatemalensis, 121, 124, 125, 126, 127
 guayaquilensis, 127
 haematogaster, 127
 leucopogon, 121, 125, 126, 127
 melanoleucos, 121, 124, 125, 126
 pollens, 127
 robustus, 121, 125, 126, 127
 rubricollis, 122, 128
Phoebe, Eastern, 77, 81, 463-464
Phoenicurus phoenicurus, 283
Phylloscopus trivirgatus, 40
 trochilus, 160
Physiology, 294-303, 400-419
Pica pica, 374
Pipilo erythrophthalmus, 60, 77, 81
Piranga ludoviciana, 94
 olivacea, 81
Pitouhui dichrous, 41, 45
Plautus alle, 289
Ploceus melanocephalus, 283
Podiceps auritus, 334
Poephila bichenovi, 279, 283
 guttata, 281, 283
Polysticta stelleri, 147
Pooecetes gramineus, 376, 465
Populations, 23-26, 66, 67, 79-82, 88-90, 95-96, 138-141, 158-166, 370-382, 391-399
Porzana carolina, 206
Predation, 57, 95, 130-157, 261-263, 305-307, 329-330, 386-387, 465
Proagriocharis gen. nov., 214
 kemballensis, 215, 216, 217
Psittaculirostris desmarestii, 31, 40, 44, 45
Pterocnemia pennata, 219
Ptilinopus perlatus, 39
 pulchellus, 39
 ornatus, 39
 rivoli, 39
 superbus, 39
Ptychoramphus aleutica, 290, 292
Publication Notes and Notices, 239, 314, 319
Puffin, Horned, 289, 291
Pycnopygius cinereus, 43, 45, 46, 50
 ixoides, 34, 35, 43, 47, 49, 50
Pyrocephalus rubinus, 315
Pyrrhula pyrrhula, 284
Quail, California, 206
Quelea quelea, 272, 274
Quiscalus quiscula, 283
Racer, Blue, 262, 306
Rail, Virginia, 206-213
Rallus limicola, 206
Rangifer caribou, 134
Rat, Cotton, 263
Razorbill, 289
Raven, Common, 386, 387, 389
Redhead, 320-323
Redstart, American, 167-176, 375
Regulus satrapa, 464
Reilly, Edgar M., Jr., The Audubon Illustrated Handbook of American Birds, reviewed, 109-111
Rhea, Darwin's, 219-220
Richmondia cardinalis, 77, 83, 330
Riedesel, Marvin L., see Hoff, C. Clayton, and ———
Rissa tridactyla, 137
Robin, 79, 80, 81, 82, 375, 378, 379
 American, 60
Roseberry, John L., and W. D. Klimstra. The nesting ecology and reproductive performance of the Eastern Meadowlark, 243-267
Ryder, John P., A possible factor in the evolution of clutch size in Ross' Goose, 5-13
Rynchops nigra, 100, 222
Salpinctes obsoletus, 375
Sandplover, Kittlitz, 100
Sayornis phoebe, 77, 81
Saxicola rubetra, 283
Scaup, Lesser, 387
Schroeder, Albert H., editor, Collected papers in honor of Lyndon Lane Hargrave, reviewed, 239-240
Scolopax rusticola, 327
Sealy, Spencer G., Egg-teeth and hatching methods in some alcids, 289-293
Sebeck, Thomas A., editor, Animal Com-

- munication: Technique of Study and Results of Research, reviewed, 240
- Seiurus aurocapillus*, 77, 80, 167, 228, 248, 283
- motacilla*, 228
- noveboracensis, notabilis*, 93
- n. noveboracensis*, 93
- n. uliginosus*, 94
- Selasphorus rufus*, 285
- Serinus*, 284
- canaria*, 285
- Service, William, Owl, reviewed, 342
- Setophaga ruticilla*, 167, 283, 285, 375
- Sex Ratios, 294-303
- Sharp, Brian, A population estimate of the Dusky Seaside Sparrow, 158-166
- Short, Lester L., The habits and relationships of the Magellanic Woodpecker, 115-129
- Shrike, Loggerhead, 375, 378, 466
- Sialia sialis*, 283
- Sigmodon hispidus*, 263
- Siskin, Pine, 464, 465
- Sitagra melanocephalus*, 283
- Sitta canadensis*, 201, 205
- c. canadensis*, 204, 205
- c. clariterga*, 201, 204, 205
- carolinensis*, 81, 286
- Skaar, P. D., Birds of the Bozeman Latilong, reviewed, 319
- Skimmer, Black, 100, 222
- Skunk, Striped, 261, 262
- Smith, Frank B., Las Aves de Tikal, reviewed, 314
- Snake, Black Rat, 306, 329-330
- Carter, 95, 261
- Prairie King, 262
- Sora, 206-213
- Southern, William E., Marsh Hawk chases crows mobbing owl, 98-99; En route behavior of homing Herring Gulls as determined by radio-tracking, 189-200
- Sparrow, Brewer's, 376, 377, 380, 381
- Chipping, 81, 376, 378
- Dusky Seaside, 158-166
- Golden-crowned, 332
- Grasshopper, 376, 379
- House, 268-278, 463, 465
- Lark, 304-309, 373, 376, 377, 378, 380, 381
- New Smyrna Seaside, 163
- Seaside, 225
- Song, 60, 246, 259
- Vesper, 376, 465
- White-crowned, 332
- White-throated, 102-103, 332
- Speotyto cunicularia*, 333, 334
- c. intermedia**, 333, 334
- c. megalospeza*, 334
- megalospeza*, 333, 334
- Sphyrapicus varius*, 282
- Spinus pinus*, 464, 465
- tristis*, 277, 284, 375
- Spofford, Sally H., review by, 342
- Spizella arborea*, 284
- breweri*, 376
- passerina*, 81, 284, 376
- Starling, 269, 276, 375, 379, 391-399, 463
- Stefanski, Raymond A., see Dixon, Keith L. and ———
- Sterna dougallii*, 99
- forsteri*, 435
- hirundo*, 99, 284, 464
- paradisaea*, 99, 383
- sandvichensis*, 284
- Stercorarius parasiticus*, 134, 386
- potanarius*, 130
- Sturnella magna*, 164, 243, 247, 257, 260
- neglecta*, 243, 237, 257, 260, 375
- Sturnus vulgaris*, 269, 283, 375, 391
- Svensson, Lars, Identification Guide to European Passerines, reviewed, 319
- Swain, Peter, see Bergman, Robert D. and ———
- Swallow, Barn, 463-464
- Cliff, 374
- Violet-green, 93, 315
- Swan, Mute, 324
- Trumpeter, 324-325, 334
- Sylvia atricapilla*, 283
- borin*, 160
- communis*, 283
- Synthliboramphus antiguum*, 290, 291
- wuuzisume*, 290
- Tachycineta thalassina*, 315
- t. lepida*, 93
- Takahe, 158
- Tanager, Rufous-crowned, 228
- Scarlet, 81
- Western, 94

- Tangara cayana*, 228
- Tate, James, Jr., review by, 239; see
Martin, Larry D., and ———
- Taxonomy, 70, 71, 93-94, 123-128, 204-
205, 355-369
- Taylor, Walter Kingsley, The double-
scratch in the genus *Poocetes*, 465;
Giant waterbug in an owl pellet, 462-
463
- Taylor, Walter Kingsley, and Hugh Han-
son, Observations on the breeding
biology of the Vermilion Flycatcher in
Arizona, 315-319
- Teal, Blue-winged, 333, 334, 447
Green-winged, 461-462
- Terborgh, John, and Jared Diamond, Niche
overlap in feeding assemblages of New
Guinea birds, 29-52
- Tern, Arctic, 99, 383-390
Black, 435-444
Common, 99, 100, 464
Forster's, 435-444
Roseate, 99
- Terres, John K., From Laurel Hill to
Siler's Bog. The walking adventures
of a naturalist, reviewed, 341-342;
Songbirds in Your Garden, reviewed,
240
- Territory, 167-176, 177-183, 327-328, 446
- Thamnophis* sp., 95
sirtalis, 261
- Thrasher, Brown, 74, 75, 77, 78, 80, 81, 330,
331, 375
Pearly-eyed, 464
- Thrush, Gray-checked, 226
Hermit, 103, 226
Swainson's, 226, 375, 379
Wood, 81
- Timken, Richard L., Food habits and feed-
ing behavior of the Baltimore Oriole in
Costa Rica, 184-188
- Tit, Blue, 271, 429
Great, 429, 430
- Titmouse, Plain, 60
Tufted, 81, 177-183
- Todirostrum cinereum finitimum*, 93
- Tody-Flycatcher, Common, 93
- Tolonen, Karl Eric, Ring-billed Gull and
Laughing Gull catch fish by "plough-
ing" and "skimming," 222-223
- Totanus melanoleucus*, 222
- Towhee, Rufous-sided, 60, 77, 80, 81, 375,
379
- Toxorhamphus iliolophus*, 31, 32, 33, 34,
35, 42, 49
- Toxostoma curvirostre*, 282, 285
rufum, 74, 81, 330, 375
- Trichoglossus haematodus*, 31, 34, 35, 39,
44, 47, 49
- Troglodytes aedon*, 375
troglodytes, 282
- Turdus migratorius*, 60, 81, 283, 375
- Turkey, 465
- Turnstone, Ruddy, 99
- Twiest, Gilbert, see Holcomb, Larry C.,
and ———
- Tyrannus tyrannus*, 374
verticalis, 93, 374
- Tyto alba hellmayri*, 101
- Urocyon cinereoargenteus*, 262
- Uria* sp., 18, 292
aalge, 289, 290
lomvia, 289
- Van Wormer, Joe, The world of the Canada
Goose, reviewed, 239
- Veery, 226, 375, 379
- Vermivora celata orestera*, 93
luciae, 315
ruficapilla, 103
r. ruficapilla, 93
- Vireo bellii*, 283, 307
olivaceus, 81, 283, 375
solitarius, 81
- Vireo, Bell's, 307
Red-eyed, 80, 81, 375
Solitary, 81
- Voicc, 53-62, 83-91, 121-123, 167-176, 315-
316
- Vole, Prairie, 262
Tundra, 133
- Von Helversen, O., see Bauer, W., and
———
- Vulpes vulpes*, 261
- Vulture, Black, 462
Turkey, 462
- Walcbeck, Kenneth C., Nesting bird ecology
of four plant communities in the
Missouri River Breaks, Montana, 370-
382
- Warbler, Audubon's, 315, 355-369

- Blackburnian, 81, 400, 405, 416
 Canada, 103
 Chestnut-sided, 81
 Garden, 160
 Hermit, 464
 Kentucky, 228
 Kirtland's, 76, 77
 Lucy's, 315
 Myrtle, 355-369
 Nashville, 93, 103
 Orange-crowned, 93
 Prairie, 281
 Swainson's, 228
 Willow, 160
 Wilson's, 94
 Worm-eating, 228
 Yellow, 174, 281, 375, 379
 Waterthrush, Louisiana, 228
 Northern, 93
 Watson, John R., Dominance-subordination
 in eaged groups of House Sparrows,
 268-278
 Wauer, Roland H., A second Swallow-tailed
 Kite record for Trans-Pecos Texas, 462
 Waxwing, Cedar, 80, 81, 375, 465
 Weasel, 261
 Least, 134, 151
 Weeks, Harmon P., Jr., Eastern Phoebe
 nesting in old Barn Swallow nest, 463-
 464
 Weeks, Sam E., review by, 112
 Weights, 19, 123, 297, 299, 300, 425
 Weisbrod, A. R., Food preferences of a
 hand-raised Blue Jay, 101-102
 Weller, Milton W., Additional notes on
 the plumages of the Redhead (*Aythya*
 americana), 320-323; see Bergman,
 Robert D., and ———
 Widgeon, American, 464
 Wilson Ornithological Society, Josselyn Van
 Tyne Memorial Library, 103; Louis
 Agassiz Fuertes Award, 469; Mem-
 bership, 200; Officers, 474; Ornitho-
 logical News, 104, 229, 335, 467-469;
 Proceedings of the Annual Meeting,
 343-352
Wilsonia canadensis, 103
 pusilla pileolata, 94
 p. pusilla, 94
 Wolhuter, Bruce R., and Frank Kish,
 Courtship display observed between
 two species of buteos, 96-97
 Wood, Merrill, A Bird-banders guide to
 determination of age and sex of se-
 lected species, reviewed, 339-341
 Woodcock, American, 161, 327-328
 European, 327, 328
 Woodpecker, Downy, 374, 379
 Imperial, 124
 Ivory-billed, 124, 128
 Linneated, 92
 Magellanic, 115-129
 Pileated, 463
 Red-bellied, 463
 Striped, 115
 Woolfenden, Glen E., A putative skeletal
 specimen of the Flammulated Owl with
 Alabama locality data, 223-224
 Wren, Cactus, 160
 House, 375, 379
 Rock, 375
Xanthocephalus xanthocephalus, 283
Xanthotis chrysotis, 31, 33, 34, 35, 42, 45,
 46, 47, 48, 50
 polygramma, 31, 32, 33, 34, 35, 42, 47, 48,
 50
 Yellowlegs, Greater, 22
 Yellowthroat, 281, 375, 379, 464-465
Zenaidura macroura, 96, 284, 374
 Zohrer, James J., Observations on pre-
 migratory movements of hand-reared
 Mallards, 323-324; see Nellis, Carl M.,
 and ———
Zonotrichia albicollis, 102, 332
 atricapilla, 332
 leucophrys, 332
 l. gaubelii, 331-332
 leucophrys × *Z. albicollis*, 331
Zosterops minor, 31, 34, 35, 43, 47, 49

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PLAN TO ATTEND THE 1971 ANNUAL MEETING

The 1971 meeting of the Wilson Ornithological Society will be held jointly with the Alabama Ornithological Society on Dauphin Island, Alabama from Thursday, 22 April to Sunday, 25 April 1971. Transportation to the Island from the Mobile airport, 30 miles north, is being arranged by Mobile members of A.O.S. Chairman of the local committee for arrangements is Dr. M. Wilson Gaillard, 319 S. Sage Ave., Mobile, Ala. 36606. Detailed information concerning accommodations, transportation, and a call for papers will be sent to all members with advance registration forms. Accommodations include a Holiday Inn, registration headquarters (it will be warm enough to swim in the pool or the Gulf) and camping grounds with water and electricity. For efficiency apartments, ideal for families, write Mrs. Caroline Hager, an A.O.S. member, 130 Mississippi St., Dauphin Island, Ala. 36528. Rates are reasonable at this season.

Dauphin Island is a narrow barrier sand island with 4 miles of pine interspersed with live oak and gum ponds and 10 miles of spartina salt marsh and beach. It is a resort, 30 miles due south of Mobile, built around a historic fishing village settled before Mobile or New Orleans.

The Island is the first landfall for millions of trans-Gulf migrants from Central America. The period 20 April to 10 May is the peak when an active birder can record 80–120 species in one full day just on the island. The A.O.S. annual meeting held here every year by popular demand usually produces a bird list of over 170 species. The 6-year list (1964–69) contains 227 species. Those interesting species seen at least five times include Magnificent Frigatebird, Gannet, Cattle Egret, Am. Oystercatcher, Wilson's Plover, Gull-billed Tern, Royal Tern, Sandwich Tern, Chuck-will's-widow, Gray Kingbird (nests), 19 species of warblers, Blue Grosbeak, and Painted Bunting. Seen at least once are Red-throated Loon, Brown Booby, Glossy Ibis, Mottled Duck (nests), Surf Scoter, Mississippi Kite, Purple Gallinule (3), Snowy Plover, Long-billed Curlew, Black-necked Stilt, Ground Dove (3), Swainson's Warbler, Lawrence's Warbler, Audubon's Warbler, Lark Sparrow. Other interesting species seen in late April on the Island include Eared Grebe, Reddish Egret, Swallow-tailed Kite, Western Kingbird, Bell's Vireo, Black-whiskered Vireo, Black-throated Gray Warbler, and Western Tanager.

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Varner, Don G., Rt. 1, Morrisonville, Ill. 62546	1964
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Verner, Jared, Dept. of Biology, Central Washington State College, Ellensburg, Wash. 98926	1964
Vesey, George W., 1447 Medford Lane, Mishawaka, Ind. 46544	1962
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Via, Jerry Waller, 3321 Courtland Rd., N.W., Roanoke, Va. 24012	1969
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Vore, Marvin E(imer), 1128 N. 8th Ave., West Bend, Wisc. 53095	1947
Wachenfeld, Mrs. Anne W., 787 E. Clarke Place, Orange, N.J. 07050	1954
Waechter, Richard F(redrick), Indiana Univ. of Penna., Indiana, Penna. 15701	1968
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Wallace, Gary Owen, Taliwa Court Addition, Apt. 175, Knoxville, Tenn. 37920	1966
Wallace, George J(ohn), Dept. of Zoology, Michigan State Univ., East Lansing, Mich. 48823	1937
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Warburton, Mrs. (J.) Mabel, 44 Hilltop Rd., Yardley, Pa. 19067	1968
Ward, Gertrude L(uckhardt), Earlham College, Richmond, Ind. 47374	1953
Ward, Rodman, 55 Selborne Dr., Wilmington, Del. 19807	1964
Warner, Alex, 133 N. Lincoln St., Kent, Ohio 44240	1963
Warter, Stuart L., Dept. of Biology, California State College, Long Beach, Calif. 90801	1956
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Columbus, Ohio 43214 1962
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Iowa 52403 1944
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20906 1954
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Wilson, Gordon, 1434 Chestnut St., Bowling Green, Ky. 42101	1920
Wilson, Harold Charles, Ephraim, Wisc. 54211	1938
Wilson, John Elder, Rt. 2, Clayton, N.Y. 13624	1948
Wilson, Mrs. Martha S., Rt. 3, Putney, Vt. 05346	1960
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Wilson, Mrs. Richard M., 7994 W. 47th Ave., Wheat Ridge, Colo. 80033	1962
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Wingate, David, Box 1244, Hamilton, Bermuda	1965
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Winter, Jon, Point Reyes Bird Observatory, Mesa Rd., Bolinas, Calif. 94924	1968
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Wisner, Herbert P., Biology Dept., Univ. of Oregon, Eugene, Ore. 97403	1964
Wistey, Mrs. Lorene S., South English, Iowa 52335	1944
Witmer, S(amuel) W(enger), Goshen College, Goshen, Ind. 46526	1948
Witschy, Mrs. Roy J., 2103 Ave. F., Scottsbluff, Neb. 69361	1965
Woeller, Richard L(ee), Rt. 1, Fulton, N.Y. 13069	1970
Wogen, Mrs. Bette Jane, 16908 Mayfield Ave., Roseville, Mich. 48066	1953
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Wolfarth, Floyd Parker, Rt. 2, Blairstown, N.J. 07825	1950
Wolfe, L(loyd) R(aymond), P.O. Box 11, Kerrville, Texas 78028	1962
Wolfson, Albert, Dept. of Biological Sciences, North- western Univ., Evanston, Ill. 60201	1944
Wolinski, Richard A., 3822 Plum St., Saginaw, Mich. 48601	1969
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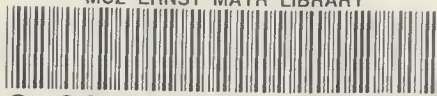
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